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Stephen R. Gliessman
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Agroecology

Researching the Ecological Basis for Sustainable Agriculture

With 87 Illustrations



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Cover: Diagrammatic representation of a corn/bean/squash intercropping system. Arrows indicate multiplicity of interactions between agroecosystem components and plants. Illustration by Annaliese Miller.

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Preface

The idea for this book developed when the Third International Congress of Ecology planned for Poland in 1982 had to be cancelled. In the two previous Congresses (1974, 1978), ecological research in agricultural ecosystems had begun to emerge as an important area of activity. I had been asked by Frank Golley, current President of the International Association of Ecology (INTECOL), which organizes the Congress, to plan a symposium on research in agroecology for the 1982 Congress. After the cancellation, I began to organize this book. Interestingly, in 1982 most of the research in this emerging field was taking place in so-called “developing countries” of the tropics. It seemed as if the value of an ecological approach to agriculture had gained early recognition in tropical areas of the world, because of the combined pressures of the tropical environment and the necessity to develop food production systems that depended less on the purchase of costly, usually imported inputs.

Over the next several years, I began to assemble the chapters for this book. When INTECOL held its international congress in Syracuse, New York, in August 1986, several symposia were organized to explore research in agroecology. Updates and new contributors to this book were made possible by these meetings. On the one hand, there was evidence of strong advances continuing to be made in the tropics. In addition, the emerging interest in agroecosystem studies in temperate regions was well represented. Temperate researchers were in the formative stages of de-

veloping a research agenda. Their presentations were conceptual in nature, rather than applied to specific agricultural situations. Their counterparts in the tropics had made considerable progress in applying agroecology to understanding the structure and function of agroecosystems, and in trying to help solve some of the problems that these production systems faced.

Fortunately, these differences recently have been diminished considerably. Agronomists and ecologists, once rarely willing (or able) to work together, have begun to bring their respective strengths and approaches together to address the serious problems that test the ability of our world to sustain its food production systems. Out of this is emerging the field of agroecology. It is hoped that this book, by presenting a series of research cases, will contribute to agroecology by providing an approach to researching the ecological basis of agricultural sustainability.

Many people helped write this book. I am especially indebted to all of the authors, and thank them for their patience and willingness to accept the challenge of showing how research in agroecology is done and why it is important. I also acknowledge the growing number of people now working in agroecological research who are not included here. I am very grateful to Frank Golley for his constant support, well-directed suggestions, and desire to have agroecology achieve broad application. Mark Lipson, Jan Ambrosini, Mary James, John Farrell, Martha Brown, Ana Chou, and Kima Muiretta all played important roles in typing, editing, and completing the preparation of the manuscripts. Annaliese Miller drew the cover illustration. Katherine Noonan at Science Tech did an excellent job of converting the manuscripts into a book. To my colleagues at UCSC in the Board of Environmental Studies and on the staff of the Agroecology Program, I am extremely grateful for their support over the last several years. I am especially thankful for the unconditional support I have received from the group Superglue. Valuable financial assistance was provided by the Alfred Heller Chair in Agroecology, the Columbia Foundation, and the W.K. Kellogg National Fellowship Program.

Stephen R. Gliessman

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1. Basic Ecological Concepts in Agroecosystems

1. Agroecology: Researching the Ecological Basis for Sustainable Agriculture

Stephen R. Gliessman

1.1 Introduction

There has been a recent emergence in research activity on the ecology of agricultural systems. After a long history of separation and lack of interaction, ecologists and agronomists have begun to combine forces to study and help solve the problems confronting our food production systems. Out of this the field of agroecology has begun to form. But as the field forms, considerable discussion and even controversy has surfaced as to how a research approach or methodology might best be applied to ensure the achievement of ecologically significant as well as agriculturally applicable results. It is one thing to gain an understanding of what makes an agroecosystem function, yet it is quite another to apply such knowledge to solving everyday problems faced by farmers around the world.

Over the past several years, a few key books have been produced that have attempted to help establish the field of agroecology, and to define more clearly the conceptual approach necessary to do research. For most of us in the field at this time, it was the book of Cox and Atkins (1979) that served an important role in both teaching and research by identifying the ecological problems in agriculture. It also was useful for identifying where research needed to be done to solve those problems. Although an ecosystem approach to agriculture was discussed, the book did not delve much into the methodologies or the ecological concepts that have been researched so actively in natural ecosystems (e.g., diversity theory, coe-

volution, allelochemicals, resource partitioning, etc.). The authors state that "agricultural activities have become the dominant ecological force over nearly one-third of the land areas of the earth." In order to help mitigate the impact of this force, their intent was to "stimulate an interest in agricultural ecology" and help "reveal the ecological fitness of past and present agricultural systems as a basis for developing an ecologically sound approach to agriculture in the future."

A few years later, Altieri (1983, 1987) published a short treatise on agroecology. He cast the book in the direction of the exploration of "the scientific basis of alternative agriculture". Rather than dwelling so heavily on the problems of modern conventional agriculture, his book went much further in describing a theoretical foundation for the study of agricultural ecology by presenting examples of agroecosystems that incorporate the concepts of ecology into their design and management. His examples ranged from traditional Third World agroecosystems to small-scale alternative and organic systems in developed countries. He gave the reader a very important perspective on what ecologically based design and management criteria are like in agroecosystems crossing a wide range of crop types and geographic regions. Rather than discuss research methodologies, though, he reported on a series of studies that explored the ecological basis of insect pest, pathogen, and weed management alternatives. For example, he proposed a three-tiered approach for bringing the agroecosystem concept to pest management: (1) use the biogeographic region, rather than a single field, as the unit for pest management research; (2) use natural ecosystems as models for pest management strategies in agroecosystems; and (3) use the understanding of interactions between plants, insect herbivores, and their natural enemies for clues to improving biological control systems. The general approach he proposes for an ecologically based pest management program prevents pest outbreaks by improving the overall stability of the system, rather than only trying to deal with pest problems after they occur. Some equilibrium needs to be established and maintained. Such knowledge can only come from effective and well directed research approaches that are based on ecosystem methodologies and concepts.

The next year a volume was published that attempted to synthesize the concepts unifying ecology and agriculture (Lowrance et al., 1984). Chapters of this book represented individual presentations at a symposium on agricultural ecosystems. The major theme of the volume was "the application of an ecosystem paradigm to agricultural science." Agroecosystems research is seen as beginning to emerge "as an innovative and holistic science concerned with both basic and applied hypotheses." The editors of the volume discuss the overspecialization and reductionism that have forced agricultural scientists to overemphasize technological applications that appear to have surpassed fundamental information. There is not sufficient information about how or why the systems func-

tion. For their own part, ecologists have not communicated or applied information to agriculture. Ecologists have been reluctant to use the agroecosystem as a basic unit of study. The great complexity of both natural and social factors is difficult to manage in ecological studies. The volume presents ideas that help reconcile these differences, and at the same time present a framework in which agroecosystems can be analyzed and modeled, so that the overall structure of systems reflects the interactions of the component parts. We are left, then, with the challenge of beginning the integrative and interdisciplinary research that will provide the basis for establishing long-term stability and sustainability of both the natural resource base upon which agriculture depends and the cultural systems with which they interact. It is the purpose of the present volume to develop a research approach, as well as give examples of this research, that addresses issues, factors, and concepts within an agroecosystem framework.

1.2 The Agroecosystem

The recent emergence of the agroecosystem concept provides a very useful means of carrying out research that attempts to integrate the multiple factors affecting agricultural systems (Spedding, 1975; Hernandez, 1977; Loucks, 1977; Hart, 1979; Lambert, 1981; Conway, 1981; Altieri, 1983; Lowrance et al., 1984). It is useful to remember that the central concept for such an approach is the ecosystem, defined as a functional system of complementary relations between living organisms and their environment, delimited by arbitrarily chosen boundaries, which in space and time appear to maintain a steady yet dynamic equilibrium. In setting up research directions that build upon the ecosystem concept as defined, it is useful to examine the chief characteristics of natural ecosystems that teach us about the interrelationships between structural and functional components. Differences between natural- and agroecosystems are introduced with human manipulation and alteration of the ecosystem for the purpose of establishing agricultural production.

Energy Flow

A well-developed ecosystem (close to the so-called climax) is relatively stable, self-sustaining, and able to maintain productivity from inputs of solar radiation (Figure 1.1). Energy flows through the system as a result of complex sets of trophic interactions. Certain amounts of energy are dissipated at different stages along the food chain, with the greatest amount of energy in the system moving along the detritus pathway (Odum, 1971). Outputs from the system can be calculated in terms of net primary productivity or biomass, each component with its corresponding energy content.

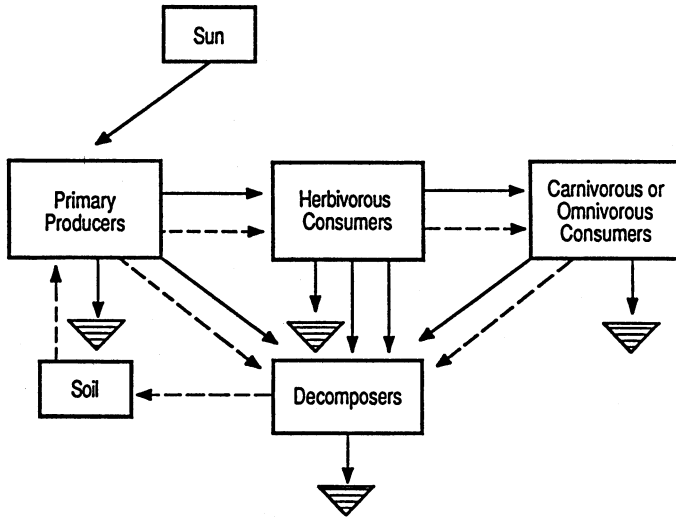


Figure 1.1. Diagram of energy flow (solid line) and nutrient cycling (dotted line) in a natural ecosystem. Arrows leading to triangles represent energy sinks (adapted from Lambert, 1981).

Energy flow in agroecosystems is altered greatly by human interference (Rappaport, 1971; Pimentel and Hall, 1984). Inputs are derived primarily from human sources and are often not self-sustaining. They become open systems where considerable energy is directed out of the system at the time of each harvest, rather than stored in biomass that could otherwise accumulate within the system (Figure 1.2).

Nutrient Cycles

Through complex sets of interconnected cycles, micro- and macronutrients circulate within the ecosystem, where they are most often bound in organic matter (Borman and Likens, 1967). Biological components of each system become very important in determining how efficiently nutrients move, ensuring that a minimum are lost from the system. Productivity is linked very closely to the rates at which nutrients are able to be recycled.

In an agroecosystem, recycling of nutrients is minimal, and considerable quantities are lost with the harvest or as a result of leaching or erosion, because of a great reduction in permanent biomass levels held within the system (Gliessman and Amador, 1980). The frequent exposure of bare soil between crop plants or between cropping seasons also creates “leaks” of nutrients from the system. Farmers have recently come to rely heavily upon petroleum-based nutrient inputs to replace these losses.

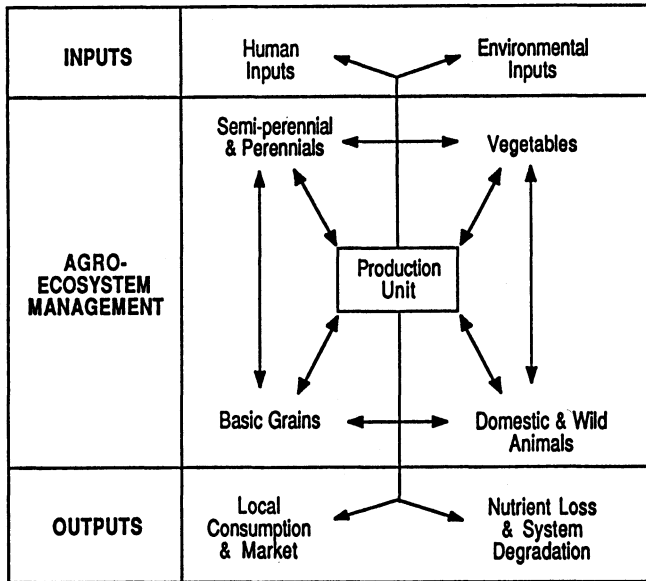


Figure 1.2. Diagrammatic representation of an agroecosystem, with an emphasis on increasing environmental inputs, as well as a reducing outputs (losses), achieved through ecological management practices (Gliessman and Amador, 1980).

Population Regulating Mechanisms

Through a complex combination of biotic interactions and limits set by the availability of physical resources, population levels of the various organisms are controlled. This population control is subsequently linked to the productivity of the ecosystem. Selection through time has tended towards the establishment of the most complex structure biologically possible within the limits set by the environment, permitting the establishment of diverse trophic interactions and niche diversification.

Because of the loss of niche diversity and a reduction in trophic interactions in agroecosystems, populations of crop plants or animals are rarely self-reproducing or self-regulating. Human inputs in the form of seed or control agents, often dependent on large energy subsidies, determine population sizes. Biological diversity is reduced, trophic structures tend to become simplified, and many niches are left unoccupied. The danger of catastrophic pest or disease outbreak is high, often despite the availability of intensive human interference.

Dynamic Equilibrium

The species richness or diversity of mature ecosystems permits a degree of resistance to all but very damaging perturbations. In many cases, pe-

riodic disturbances ensure the highest diversity, and even the highest productivity (Connell, 1978). System stability is not a steady state, but a dynamic and highly fluctuating one that permits ecosystem recovery following disturbance. This permits the establishment of an ecological equilibrium that functions on the basis of sustained resource use, which the ecosystem can maintain indefinitely, or shift if the environment changes or is altered.

Because of the reduction of structural and functional diversity, much of the resilience of the agroecosystem is lost, and constant external inputs must be maintained through human interference. A focus on harvest outputs upsets the former equilibrium, and can only be sustained if such outside interference continues.

1.3 An Agroecological Approach to Research

Once an ecosystem is disturbed for the purpose of converting it into an agroecosystem, the original equilibrium and resilience is altered and replaced by something that reflects a combination of ecological and socio-economic constraints. The challenge for agroecology, then, is to find a research approach that consciously reflects the nature of agriculture as the coevolution between culture and environment, both in the past and the present. The concept of the agroecosystem can (and should) be expanded, restricted, or altered, as a response to the dynamic relationship of human cultures and their physical, biological, and social environments. An understanding of this relationship provides a framework in which inputs, outputs, and sustainable production processes can be maintained. The chapters of this volume present this type of broad and integrated approach to research in agroecology. They are intended to provide an example of the framework possible for doing effective research on agroecosystems, and a broad range of topics is covered. By no means are all of the possible topics covered. It is the intention of this volume to present a context for future research in agroecology, with examples of how such research is carried out, so that we can stimulate the much-needed research efforts that will integrate disciplines and hasten the transition to sustainable agricultural practices everywhere.

The book is divided into two sections. The chapters presented in the first section focus on the study of basic ecological concepts as they function in or apply to agroecosystems. The examination of the four characteristics of agroecosystems mentioned above is extended to the ecological analysis of factors that eventually control levels of output production or harvest. The chapters by Letourneau, Carroll and Risch, and Power examine the various ecological concepts behind such agronomic practices as biological control and integrated pest management. Analysis of a specific pest management strategy is presented by Altieri

et al. The studies presented in the first several chapters have been carried out across a geographic range from California, to Mexico and Central America. Lumsden et al. give an ecological approach to pest reduction in soil-borne plant pathogens in rural Mexico. The concept of allelopathy is explored by Chou, with specific examples presented from extensive research on agroecosystems in Taiwan. Nutrient dynamics and the role of weeds in an agroecosystem are explored by Lambert in studies on local, traditional agroecosystems in Belize. The concept of "low-input" agroecosystems is described by Jannsens et al., based on research done in highland Africa, and Amador and Gliessman look at multiple cropping from an ecological perspective in work in the lowland tropics of Mexico. The general area of agroforestry is examined by Gliessman as a means of managing diversity in agroecosystems, with work on traditional home gardens in Costa Rica and Mexico presented as examples. Farrell explores the ecological impacts that trees can have in a particular agroecosystem in the uplands of Central Mexico. Wood and Bollinger examine more generally applicable characteristics of interactions between trees and microorganisms that are basic for improving the ecological role of trees in production systems. Finally, Vandermeer and Schultz describe a theoretical framework for analyzing complex interactions in agroecosystems, focusing on a mathematical analysis of intercropping systems, derived from their studies in Michigan and Central America.

The chapters in the second section present a broad overview of the kinds of research that need to be done to gain more understanding of the cultural components of agroecosystem design and management. In a sense, such research falls into the categories of landscape ecology or cultural ecology. The chapter by Siemens, for example, delves into the past, and through archaeological studies, examines the relationships between past and present day use of an agroecological landscape in tropical Mexico. Ramakrishnan describes the agroecosystems of a region of north-eastern India, and uses an ecological approach to gain a comparative perspective on different subsystems. Molenaar uses a historical approach to examine the impacts that water management for agriculture has had on the environment in the Netherlands. The chapters by Pimentel and Dazhong look at energy use in agriculture, an issue of much concern during the past decade, examining agroecosystems in geographical regions as diverse as the corn belt of the United States and northeastern China. Finally, attempts to set the stage for future research in agroecology are described by Trenbath et al., in work based on analytical models for sustainable agroecosystem management, and as concluding remarks by Gliessman on the ecological element in sustainable agriculture.

Again, it is not intended that every possible avenue of research in agroecology be covered in this volume. In an area of ecological research that is beginning to receive considerable attention, this volume is intended to function as an example of the directions such research should

take. The directions must integrate concepts and cross disciplines. We have learned much from studies of traditional, rural cultures around the world, as exemplified in most of the chapters in this book. Empirical knowledge has been gained through a process of trial and observation, under conditions of limited resources and strong environmental control. From these studies, we are gaining insight into how to direct research for the future. This future involves the integration of ecological and cultural knowledge. Only in this manner can agriculture establish a truly sustainable base.

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2. Two Examples of Natural Enemy Augmentation: A Consequence of Crop Diversification

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2.1 Introduction

2.1.1 Background

Inquiries concerning a general relationship between biotic and structural complexity and community stability have been approached by examining experimental communities in the laboratory (Huffaker, 1958; Hairston et al., 1968), depicting interactions with mathematical models (e.g., MacArthur, 1955; De Angelis, 1975; Gilpin and Case, 1976; Nunnery, 1980; Yodzis, 1980), in field experiments with aquatic systems (McElravy et al., 1982; Zaret, 1982), noncrop habitats (Kroh and Beaver, 1978; Wolda, 1978), and in agroecosystems (Pimentel, 1961; Trenbath, 1974; Risch, 1979). Critical reviews on the diversity/stability hypothesis have addressed both the basic aspects and their applications (Southwood and Way, 1970; Goodman, 1975; May, 1979; Pimm, 1984). Most of the experimental and empirical work in agroecosystems has concerned population patterns of component arthropod species in response to vegetational diversity. Floral diversity affects population stability, which can be defined practically as the persistence of the species in a system (Van Emden and Williams, 1974) or as the rarity of high amplitude population oscillations in the history of the community (Leigh, 1965). The assumption that this stable equilibrium level is below an economic threshold is sometimes implied as well. A sample of dicta selected from the subset

of papers on pest management in the 1970s will illustrate the state of controversy that persists in the literature. Nickel (1973), Litsinger and Moody (1976), and Perrin (1977) concluded that a reduction of vegetational diversity (as in large-scale monoculture) may allow pest population densities to increase to outbreak proportions because of decreased interference competition. Way (1976) noted, however, that the absence of alternate host plants in a monoculture may cause a dislocation of the pest's life cycle requirements and thereby prevent population outbreaks. Pimentel (1961) proposed that the greater species diversity of parasitoids and predators in mixed crop assemblages can effect greater pest population stability. Watt (1965), however, cautioned against multiple releases of natural enemies. He posited that although interspecific competition between herbivores may be a stabilizing factor, competition for resources between members of the third trophic level causes instability. Hagen and Hale (1974) advocated the integration of cultural practices, such as polyculture, with biological control efforts, although Way (1976) observed that most successful biological control programs have occurred in monoculture (though he did not specify whether his proportions are standardized by the frequency of attempts in each system).

Most investigators offer qualified opinions that planned combinations of plants are more likely to effect management of pests below an economic threshold than indiscriminate diversification of simplified systems (Way, 1966; Kennedy, 1968). Way (1979) summarized the contradictory views as "a period of clarification and confusion" and deemed critical the need for research with respect to cropping systems in the small farm setting and especially in tropical areas.

2.1.2 Vegetational Diversity and Pest Abundance: Two Hypotheses

Most experimentation designed to assess practically the importance of diversity for reducing pest population fluctuations has involved the establishment of enriched and simple crop designs, with subsequent comparison of the distribution and abundance of pest populations and natural enemies (Smith, 1969; Tahvanianen and Root, 1972; Perrin, 1977; Altieri, 1980; Bach, 1980a, b, 1984; Risch, 1980, 1981; Letourneau and Altieri, 1983; Letourneau 1986, 1987). The majority of field studies show a decrease in herbivore abundance or biomass associated with the presence of nonhost plants in diverse mixtures (Risch et al., 1983; Andow 1986). The factors underlying this "associational resistance" (Tahvanianen and Root, 1972) in taxonomically, structurally, and microclimatically complex habitats have been included in two hypotheses proposed by Root (1973).

The "Enemies Hypothesis" predicts that species-rich plant assemblages will be associated with an increased abundance and diversity of

arthropod predators and parasitoids. The emergent properties that influence three-trophic-level interactions include an increased variability of food resources (such as nectar, pollen, and alternate hosts/prey) and refugia, which serve to augment populations of natural enemies, improving both their functional and numerical responses to prey density (van den Bosch and Telford, 1964; Root, 1973; Price et al., 1980). The performance of natural enemies may also be enhanced by chemical cues from associated plants (Altieri et al., 1981; Nordlund et al., 1988).

The "Resource Concentration" hypothesis suggests that food plants occurring in pure stands will more likely be found by herbivores (especially those with narrow host ranges) and, compared to diverse associations, specialists will exhibit longer tenure time, and perhaps, higher feeding and reproductive success (Root, 1973).

Risch et al. (1983) suggest that herbivore movement patterns, rather than the action of natural enemies, account most often for higher pest abundance in simple rather than in diverse systems. The importance of natural enemies has not been established in terms of a direct relationship between diverse vegetation and better pest regulation. Much of the recent work, however, has been conducted with species or life stages of herbivores that are not particularly conducive for measuring enemy impact (Bach, 1980b; Risch, 1981; Andow, 1983).

In the following section, I summarize experiments with traditionally managed agroecosystems in the lowland, humid tropics of Mexico and on furrow-irrigated crops in the Sacramento Valley, California that demonstrate associational resistance to squash pests in intercropped corn/cowpea/squash systems. The objective of these studies was to compare the incidence and impact of natural enemies in pure stands and crop mixtures.

2.2 Maize/Bean/Squash Intercropping

Polycultures of basic food crops have been cultivated for thousands of years in Mesoamerica (Willey, et al., 1964; Pinchinat et al., 1976). In tropical Mexico, a common polyculture arrangement consists of maize, which provides support for a climbing legume, and squash vines, which form a ground cover. Agricultural practices in this region, however, are in transition. Recent changes include the mechanization of crop production and harvesting, use of high-yielding varieties, increased input of synthetic fertilizers and pesticides, and a shift from mixed cropping methods to monoculture (Janzen, 1973; Kass, 1978). The speed of this transition is dependent upon capital availability and access to credit, technology, and information on modern farming techniques (the development "package"). The smallest land holders often receive only a

small portion of these resources (Harwood, 1979; de Janvry, 1981; van Huis, 1981).

Whether as a response to mechanization or, at the other extreme, an attempt to modernize without capital expenditure, farmers tend to rely less upon traditional polyculture practices. Farmers with access to the development "package" obtain yield increases, at least in the short run. Small landholders producing subsistence crops, however, often change only the cropping pattern, as was common practice in the state of Tabasco in Mexico. A shift from polyculture to monoculture, using the same varieties, can adversely affect soil fertility (Gliessman, 1988), productivity per unit land (International Rice Research Institute (IRRI), 1974; Willey, 1979; Vandermeer, 1981), root nodule formation (Boucher and Espinosa, 1982), and can increase economic risk (Moreno and Hart, 1979; Norman et al, 1979) while influencing dietary intake (Dewey, 1979). This shift can also promote outbreaks of pest insects (Altieri and Letourneau, 1984). Altieri et al. (1978) and Risch (1980) have documented evidence that many pest species in traditional intercropped systems can be maintained at lower equilibrium levels than in monocultures of the same crops. Ninety percent of the farmers I interviewed in a Tabasco farming community had noted increases in pest problems over the past 10 years. All have simplified their crop planting patterns. The practical aspects of studying the potential of vegetational diversity for the prevention of pest population outbreaks are clear. Detailed examinations are critical in the face of the current trends toward crop field simplification and a growing need for sustainable pest management systems (Altieri et al., 1983).

2.2.1 A Test of the Enemies Hypothesis

During the wet and dry seasons of 1980 and 1981, squash in monoculture and polyculture on Mexican family farm parcels was sampled for herbivores. Field observations of predation were recorded, and herbivores were reared for parasitoids (Letourneau, 1983). The most common herbivore, *Diaphania hyalinata* L., tended to be more abundant on *Cucurbita moschata* and *C. mixta* in monoculture than when interplanted in the traditional manner with maize, *Zea mays*, and cowpea, *Vigna unguiculata*. During the second wet season, herbivore density samples were coupled with quantitative samples of beneficial species. As a test of the "Enemies Hypothesis", the abundance of hymenopteran protelean parasitoids was compared between traditional and monoculture squash cropping systems. To further test the relevance of any correlations between cropping system and propensity for high parasitoid abundance, *Diaphania hyalinata* eggs and larvae were evaluated with respect to overall parasitization rates and species richness of their parasitoid complex. Because *D. hyalinata* fly at night, the influence of resource concentration on the abundance of pests was inferred from the distribution of eggs in experimental plots.

2.2.2 Methods

Six groups of 10 m by 10 m experimental plots were randomly assigned first cropping pattern (monoculture or triculture), then ground cover (bare soil, mulch, and natural vegetation), such that each of the various cropping practices common to the local people was represented by six replications. To maximize patch size of single and mixed culture and minimize differential edge effects for ground covers, plots were randomly assigned main areas of cropping pattern and a latin square design was adopted, respectively (Figure 2.1). Parasitoid abundance was estimated from captures by Malaise traps placed centrally for 12 hours in each monoculture and polyculture at 10-day intervals.

D. hyalinata eggs and larvae were sampled by visual inspection of three randomly selected seven-leaf units of squash vegetation (leaf area not significantly different between treatments, Student's *t*-test; $p < .05$) per plot, and each specimen was collected for laboratory rearing of parasitoids. Results of herbivore samples were analyzed using a 5 factor, ANOVA: field, 2 levels; cropping pattern, 2 levels; ground cover, 3 levels; row, 3 levels; column, 3 levels on seasonal totals (because of the dependent nature of samples taken over time). The skewed distributions of egg density and proportions of eggs parasitized were made more nearly normal by square root and arcsine transformations, respectively.

2.2.3 Results

As predicted by the "Enemies Hypothesis," Malaise trap captures of parasitoids in squash monocultures consisted of fewer individuals than those in polyculture (seasonal $\bar{X}$ (mono) = 8.6 ± 1.7 SE and seasonal $\bar{X}$ (poly) = 17.8 ± 3.3 SE). Abundance patterns within treatments were similar over time. Among treatments, polyculture catches were consistently higher than those in squash monoculture (Figure 2.2, plot portion).

General comparative measures of parasitoid diversity and abundance suggest only a qualitative estimate of parasitism pressure over treatments. The relevance of this measure was checked by determining the capture rates of those species that actually attack *D. hyalinata* on squash. There was a greater representation of these species in polyculture traps (Figure 2.2, bar chart).

The mean density of *D. hyalinata* eggs was higher in monoculture until the end of the season (Figure 2.3A) when monoculture vines began to yellow and die back (ANOVA, $F(1,8) = 61.2$, $p < .01$). With respect to ground covers, egg density in mulched plots was significantly greater than in bare soil, and weedy plots had still fewer (Duncan's multiple range test, $p < .05$). Larvae showed a similar pattern (Figure 2.3B) of higher mean densities in monoculture (ANOVA, $F(1,8) = 23.6$, $p < .01$). However, ground cover did not significantly influence larval densities (ANOVA, $F(2,8) = 1.7$, $p = .24$). These analyses showed no significant in-

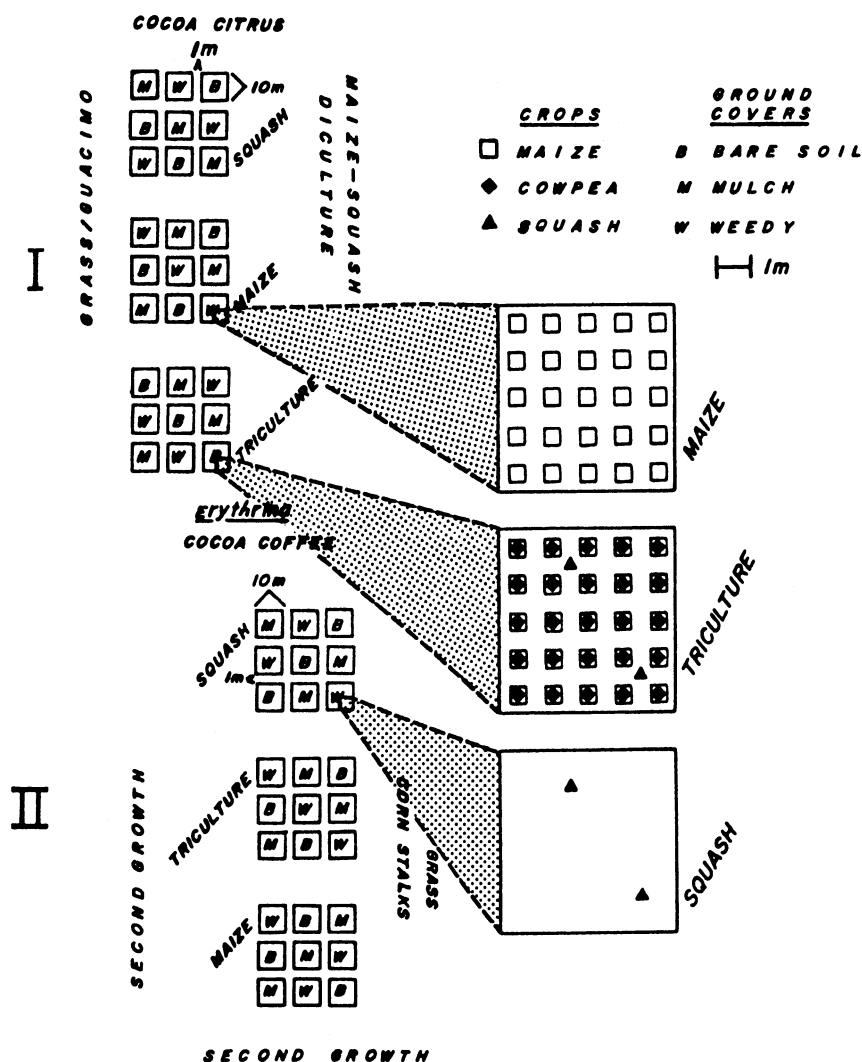


Figure 2.1. Experimental plot design with cropping represented in field I and field II. Ground covers were assigned to Latin Squares. Tricultures had the same density per crop as did monocultures.

teraction between ground cover and any other factor and no row and column effects were present.

The seasonal mean proportion of eggs parasitized (Figure 2.3A) was significantly greater in mixed culture, $\bar{X}$ (poly) = 33%, than in monoculture, $\bar{X}$ (mono) = 11% (ANOVA, $F(1,8) = 42.5$, $p < .01$).

Total parasitization of *D. hyalinata* larvae (Figure 2.3B) was higher in polyculture plots as well, $\bar{X}$ (poly) = 59% versus $\bar{X}$ (mono) = 27% (AN-

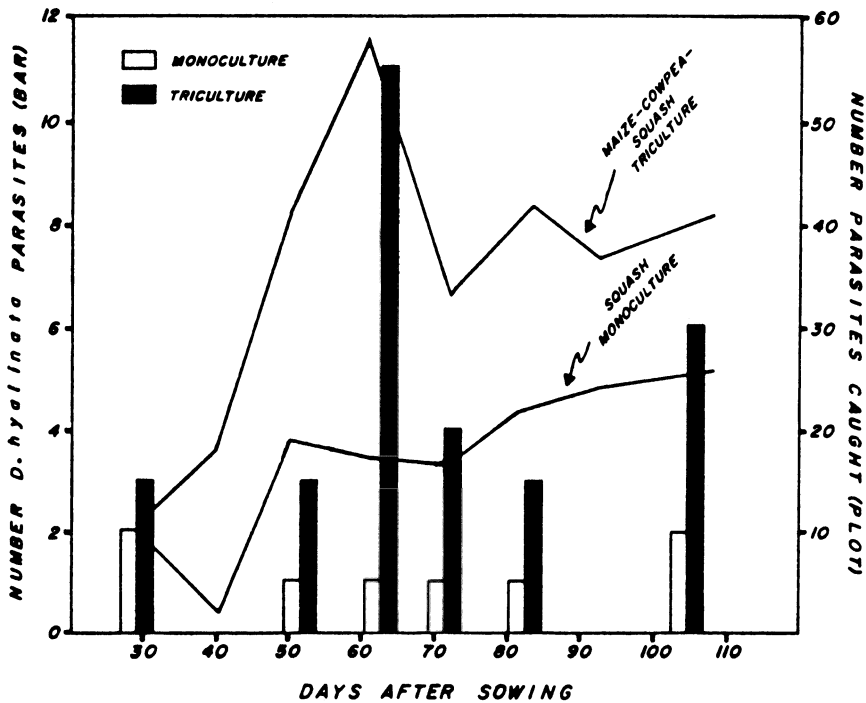


Figure 2.2. Malaise trap catches of total hymenopterous parasite catches are plotted (right y axis) and bars show the subset of those that attack *Diaphania hyalinata* in monoculture and triculture (left y axis).

OVA $F(1,8) = 39.6, p < .01$). Seven species of parasitoids were reared from the larvae.

2.2.4 Discussion

Visits of hymenopterous parasitoids, as determined by capture during flight through plots, were increased by planting mixed crop assemblages in the traditional manner rather than growing squash in pure stands. As predicted by the "Enemies Hypothesis", parasitization of a major squash pest, *D. hyalinata* was more effective in the vegetationally diverse plots. Further study, which includes the detailed biologies of the resident species, is needed to determine the exact mechanisms that influence the distribution and abundance of parasitoids in maize/bean/squash polycultures. The effects reported here are likely due to a combination of factors. A pronounced increase in parasitoid abundance when corn began to flower suggests that pollen or honeydew produced by corn aphids may have attracted additional parasitoids to polyculture plots. Presumably, most of the additional individuals captured in polyculture represent the complex of parasitoids attacking species associated with cowpea and

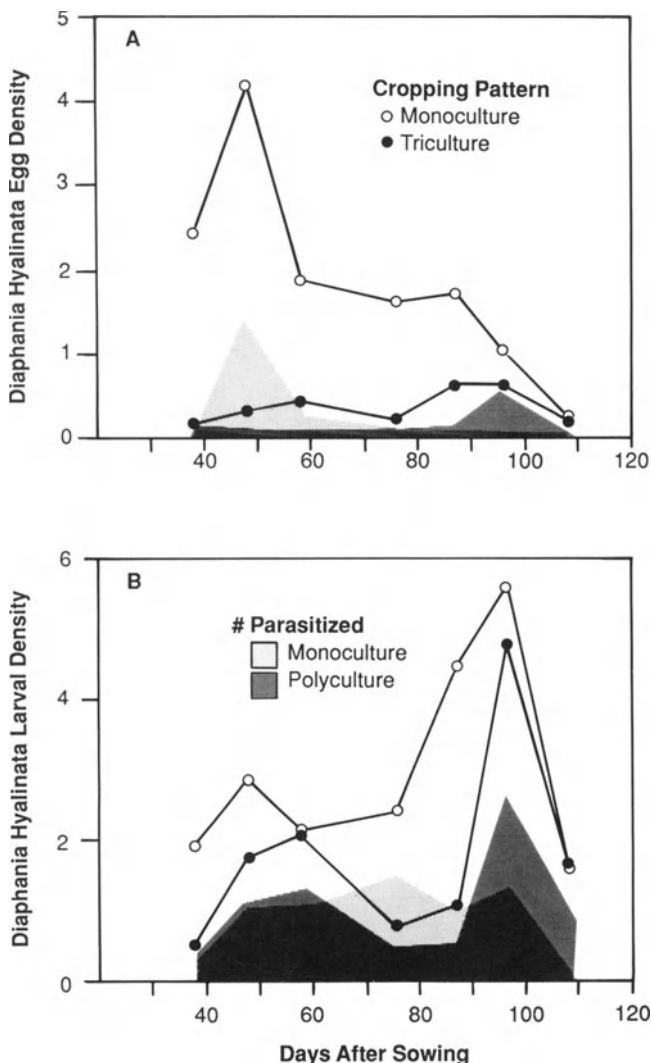


Figure 2.3. *Diaphania hyalinata* egg (A) and larval (B) densities are plotted as means of 18 plots for each sample date in monoculture and triculture. Shaded areas under the plots show the mean number of eggs (A) and larvae (B) that were parasitized in each treatment.

maize. The only evidence of host overlap between Lepidopteran species was collected for a generalist egg parasitoid. The availability of alternate food for adult and larval parasitoids, however, may not have been as important as some aspects of the structural complexity of polycultures. Additional data from maize monocultures, which have lower food var-

iability than squash monocultures, showed malaise trap captures of parasitoids were comparable to the high numbers caught in polycultures (Letourneau, 1987). The presence of maize plants in the system seems to increase its attraction or suitability for parasitic wasps.

The distribution of *D. hyalinata* eggs can be used to assess the impact of resource concentration between treatments. Shading by maize and cowpea in polyculture inhibits growth of squash, and the percentage of coverage of plots was significantly reduced in polycultures as compared to monoculture, though the number of plants was equal. Densities of eggs, standardized by squash-leaf area also support the idea that specialist herbivores colonize their host plant according to its concentration in the habitat. The tendency for squash plants in polyculture to have a lower density of immature *D. hyalinata* was likely due to both resource concentration effects and more efficient biological control by natural enemies.

2.3 Habitat Attraction and Predator-Prey Interactions in Monoculture Versus Intercropped Fields

Dempster and Coaker (1974) observed that even small changes in cropping practices can greatly alter the attractiveness of plots to a pest and its natural enemies. Rates of crop colonization by insects depend upon insect mobility, the proximity of the source of colonizers, and the attractiveness of the crop (or host/prey) at the crucial period of dispersal (Huffaker et al., 1977). Diversification of vineyards has shown that the presence of alternate prey associated with noncrop vegetation can prevent local extinction of predator species (Doutt and Nakata, 1973) or increase the proximity of colonizer sources (Flaherty, 1969).

In this second example, predator colonization rates are suggested as an aspect of pest control that can be manipulated through vegetational diversification of the crop habitat (Letourneau and Altieri, 1983).

2.3.1 Methods

Population densities of the minute pirate bug, *Orius tristicolor* (White) and its preferred prey, the western flower thrip, *Frankliniella occidentalis* (Pergande) were monitored in squash monocultures and polycultures of squash (*Cucurbita pepo*), cowpea (*Vigna sinensis*), and corn (*Zea mays*) in central California. Sixteen 14 m by 14 m plots were sown such that the density of each crop was equal among treatments (Fig. 2.4) with three replications of corn and cowpea monocultures, and between three and five replications of squash monoculture and polyculture treatments assigned to a completely randomized design. Arthropods occurring on squash foliage were sampled by visual inspection at approximately weekly

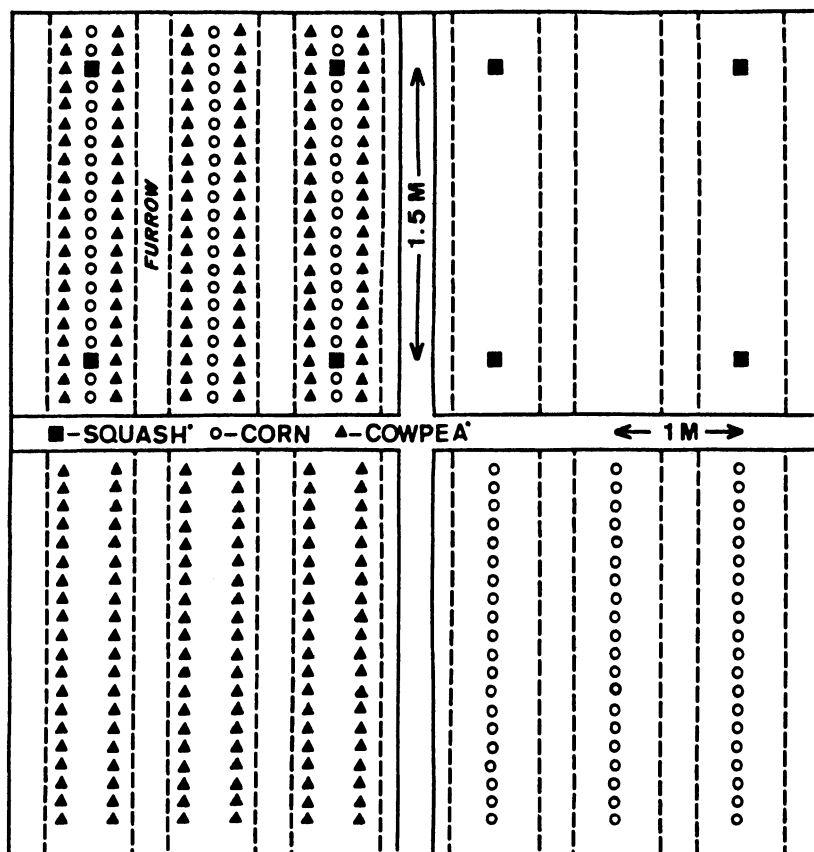


Figure 2.4. Cropping design showing spacing of young plants in monocultures and polycultures under furrow irrigation.

intervals, and numbers per plant were converted to densities per 5 g squash-leaf biomass for standardization between treatments.

Two outdoor cages were each placed over two hills of squash in monoculture so that *Orius* abundance could be manipulated within them. Thrips were sampled both inside cages and on adjacent, uncaged control plants at weekly intervals. Predator manipulations were as follows:

Day 50: *Orius* manually killed within both cages.

Day 57: Predators, equal in number to those killed previously, are captured in the field and released into cage 1.

Day 65: *Orius* (adults that invaded the fine mesh and nymphs eclosed from eggs) reexterminated manually in cage 2.

2.3.2 Results

The mean density of thrips on squash leaves was initially much greater in monoculture (Figure 2.5) and remained significantly higher until day

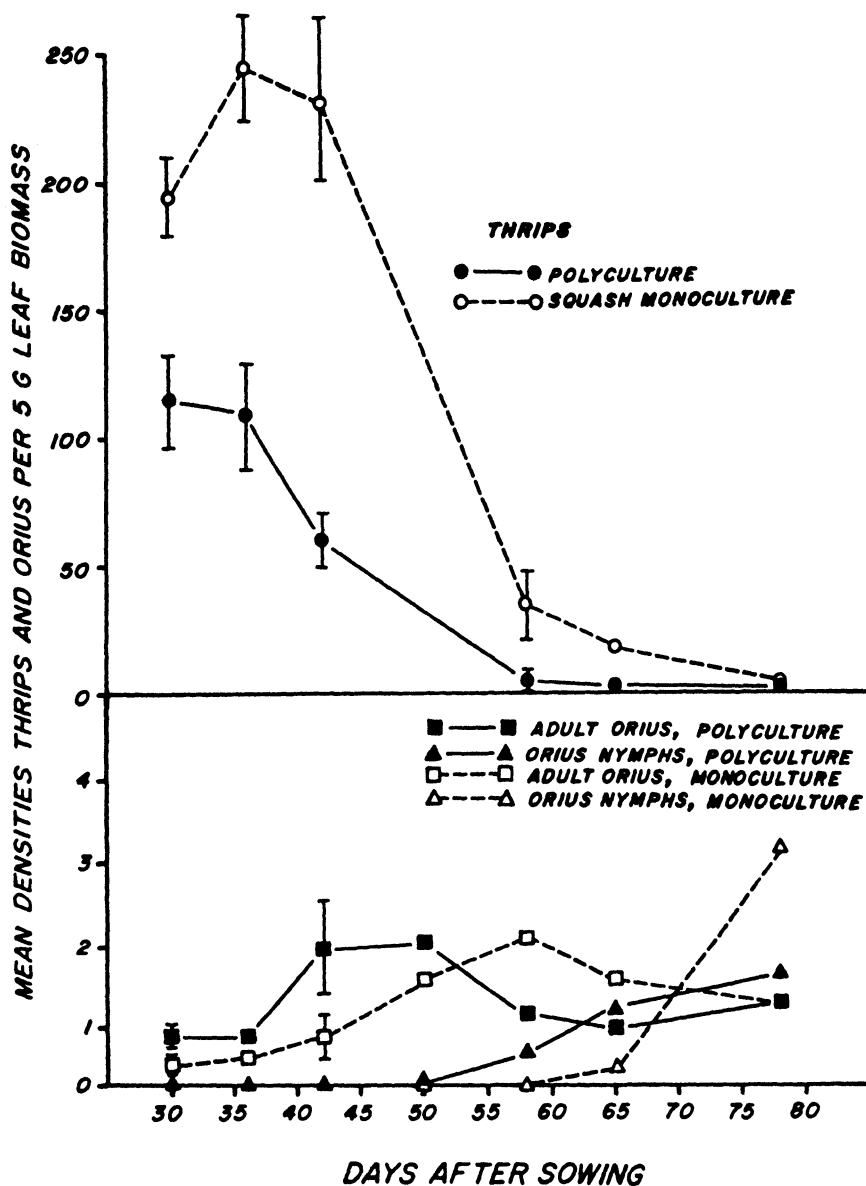


Figure 2.5. Predator-prey relationships in monoculture and polyculture plots from samples taken on squash leaves. Standard error of the mean is indicated when treatments were significantly different (ANOVA; $p < .05$).

65 after sowing (ANOVA: treatment, 2 levels; plot nested in treatment, 3 to 5 levels). *Orius* colonization however, was more rapid in polyculture (Figure 2.5). Average thrips densities decreased as predator densities increased in both treatments, but the pattern in monocultures occurred 8 to 14 days later than in polycultures.

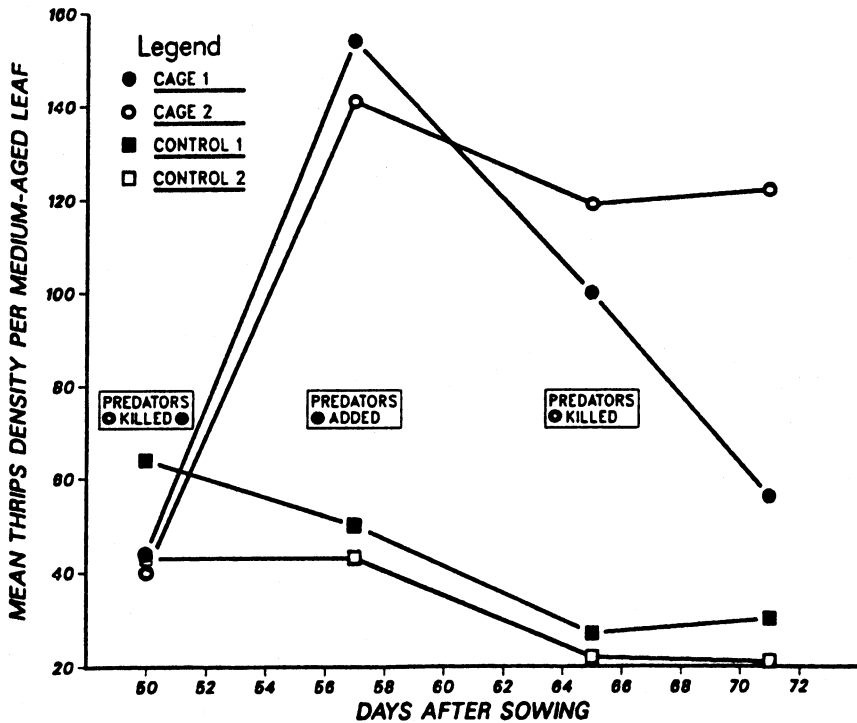


Figure 2.6. Mean density per leaf, of *Frankliniella occidentalis* in two predator-manipulation cages versus uncaged control plants near each cage in squash monoculture. Three manipulations are summarized in boxes with symbols to indicate the cage involved.

Do the typical predator/prey abundance curves in these cropping systems reflect a cause and effect relationship? Although thrips population densities declined in squash monoculture plots, their abundance more than tripled, on the average, inside cages devoid of *Orius*. Figure 2.6 illustrates the response of thrips densities to predator manipulations compared to uncaged control plants with steadily falling pest densities. Thrips densities decreased in cage 1 following the addition of predators on day 57. A smaller decrease in cage 2 (Kolmogorov-Smirnov test: $Kd = 5$, $p < .05$) may have been due to adult *Orius* that had slowly invaded through the fine mesh and nymphs that had eclosed from caged plant tissue. With a subsequent removal of predators inside cage 2 (Figure 2.6), the mean density of thrips per leaf in cage 1 further decreased as compared to that in cage 2. (Mann-Whitney U-test: $U = 0$, $p < .01$).

2.3.3 Discussion

A greater potential for pest control in the complex versus the simple crop system was demonstrated by an increased colonization rate by a generalist

predator. Presumably, *Orius* was not colonizing these crop plots in response to thrips aggregations, at least during the habitat-location phase. Smith (1976) documented a similar phenomenon involving the colonization of brussels sprouts fields by *Anthocorus nemorum* (L.) with and without weedy vegetation. Although the aphid prey occurred at higher densities in bare soil treatments, the predators were more abundant in samples from weedy areas. "Crop background" was proposed as the factor determining these trends. Rapid colonization and/or higher densities of other predator species have been found in dense vegetation as well (Sprengel et al., 1979; Horn, 1981).

Faster colonization rates of *O. tristicolor* in early-season, mixed-culture plots may have been due to a greater attractiveness of polyculture during the host habitat-location phase. Alternatively, because colonization represents not only immigration but also emigration, the increased densities of *Orius* adults may have been due to a more suitable combination of microhabitats in polycultures, once the habitat was found by this generalist predator. Leigh et al. (1974) showed both plant density and soil moisture to be positively correlated with *O. tristicolor* densities in cotton fields. In the present study, however, the early season colonization patterns probably were not due to abiotic factors, such as humidity levels and temperature, which vary much more as the plants increase in size.

Prey densities that fall below a certain threshold can cause emigration after the initial attraction of predators to an area (Hassell and Southwood, 1978). The lower density of a predaceous beetle, *Coleomegilla maculata* (De Geer), in corn/bean/squash polycultures compared to monoculture corn was explained, at least in part, by decreased foraging efficiency due to the addition of leaf area without comparable addition of prey (Risch et al., 1982). The prey density aspect of crop attractiveness is likely to vary with the predator specificity. *O. tristicolor* fed primarily on thrips in squash foliage, as a result of both the near absence of alternate prey (such as mites and aphids) and the comparatively high escape rate of *Empoasca* spp. Corn pollen, an important food source for *Orius*, was not available in polycultures until day 72. The low population densities of thrips, then, must have been sufficient to maintain *Orius* immigrants in early-season polycultures.

Further studies have recently been conducted on the mechanisms of habitat attraction. I have attempted to separate the components of polyculture, such as taxonomic richness, plant density, color/contrast, volatile chemicals, and structural complexity to understand their relative importance in terms of the colonization rates of this generalist predator (Letourneau, in press).

2.4 Conclusions

As an atypical conclusion, perhaps, I will not restate results; rather, I will pose a set of questions that are relevant to a number of papers in this

volume. What can ecological theories do for agriculture? And, conversely, what can studies with crop systems provide, in terms of testing or illustrating ecological principles? Taking a "complexity begets stability" maxim as an example of a theoretical construct, and pest regulation as a practical goal, we might assume that the current use of monoculture over large acreages would cause farmers to face the dilemma of a pest-managing Sisyphus, except that with time, the boulder is gaining mass, and the mountain is eroding. Monoculture does have important ecological costs (Horwith, 1985). But, to assess the connections we must define complexity and stability in terms of the practical goal. What are the quantitative and qualitative measures of complexity and stability? From which perspective is it measured? It is conceivable, for example, to have a very high species richness of herbivores feeding on all parts of the crop plant, with all herbivores reaching a condition of regulation through gross resource competition. The result would be a high level of commercial damage as a result of high diversity and high stability in the community. The general assumption, however, is that the mechanism of pest regulation is not linked with exploitation of the particular vegetative resource.

Even if we agree that what would loosely be expected in a complex and stable crop system is a comparatively high species richness of plants and animals that interact in some way to prevent herbivore population levels from surpassing economic thresholds, other considerations arise. Management of crop systems to be temporally discrete, nonequilibrium communities places limitations upon the usefulness of general community theory as a basis of prediction (Pimm, 1984) and upon the suitability of testing these theories in crop habitats.

The clear advantage of considering ecological theory is the synthetic approach to crop maintenance that is invoked by the method. Various control and enhancement practices are less likely to conflict if interactions and processes are monitored. The important feature of agricultural fields for ecological research is the ease of manipulation of factors and the comparative uniformity for variables that can be held constant. It is possible to vary separately structural, textural, visual, chemical, and microclimatic components of the system, without compounding variables such as temporal or spatial separation of treatments. The ease of conducting manipulative experiments can be coupled with social advantages of producing results that are directly related to the production of food and fiber. (This kind of social ranking is valid as long as access to food, fiber, knowledge, and aesthetic resources is neither equal nor sufficient among people). A common basis of criticism for the application and testing of ecological theory in agriculture is the validity of generalization. The problems with selected crops during particular seasons, under a particular complex of abiotic conditions, must be examined in a detailed manner, with reference to specified needs of target components of the system. As a point of conjecture, it may be true that a traditional maize/

bean/squash polyculture has a reduction effect for most squash pests and a augmentative effect on parasitic wasps. But if the target herbivore prefers shade and attacks young fruit, or if it attacks the seedlings when both habitats are very similar, the average or majority effect may not be critical in a practical sense. In an integrated pest management program, however, community patterns are important. Population regulation is the goal, and a wide variety of control measures are available. The difficult decisions are often associated with combining these practices in a compatible manner. By and large, the theoretical tenets of areas such as biogeography, chemical ecology, and population ecology are the guidelines, and they have contributed a great deal to the development of pest management tactics such as cultural controls, plant resistance, pesticide technology, and biological control. Critical studies such as the ones in this volume illustrate the opportunities for important work on the frontier of this interface between theory and practice.

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3. An Evaluation of Ants as Possible Candidates for Biological Control in Tropical Annual Agroecosystems

C. Ronald Carroll and Stephen Risch

3.1 Introduction

Past researchers have usually regarded the search for candidates for pest control programs as a biological problem. But pest control is essentially a social and economic problem that uses biological technology (Reichelderfer, 1981). From a farmer's perspective, the evaluation of a pest management program includes much more than the effect the introduction of a beneficial insect might contribute toward lowering pest losses below economic thresholds. Farmers are concerned with how the particular program will place restrictions on time and alternative farming practices, and thus affect opportunity costs. Pest control programs may affect production costs by decreasing opportunistic use of chemical controls and by influencing the temporal variability of yields. Thus, the biological characteristics of control agents become coupled with a farm's social and economic characteristics. For example, in a situation where pest diversity is high and individual population size variable, the introduction of a specialized predator may strongly influence the population size of one pest species. Several outcomes are possible. If competitive interactions exist among the pest species, then the elimination of one species causes compensatory competitive release among the others, but the numerical response may not be linear. Even if competition does not occur among the pest species, the elimination of one pest species may cause a change

in the population size of the other species. If the eliminated species was an important food for generalist predators early in the crop growing season, then eliminating that food item will have a negative impact on generalist predators, and may cause an increase in the populations of later pest species. From the farmer's viewpoint, the result influences average yields and temporal yield variance and assumes importance as the farmer evaluates his/her prospects for servicing next year's debt load. In this chapter, we present an overview of the social and economic environment of small-scale, tropical farmers, knowledge that is fundamental to the development of appropriate pest control programs. Following the social and economic analysis, we discuss the potential benefits and liabilities for using ants as biological control agents in tropical, annual cropping systems.

3.2 The Socioeconomic Environment

Among developing nations, credit institutions have largely ignored the needs of poorly capitalized farmers who produce a large share of domestic basic foods (Harwood, 1979; Oram et al., 1979). The pressing need to generate foreign currency has led developing countries to greatly favor the growth of cash-export crop agriculture, often allowing domestic food production to languish. The production technology of cash-export crops usually follows the model of highly industrialized western agriculture. Thus, capital credit for improving crop yields strongly favors the common "package" of mechanization, modified crop strains, synthetic fertilizers and pesticides. Clearly, the large-scale producer benefits by the artificial economies of scale that are created by these support programs. For small-scale farmers, programs that improve access to this technology package are, at best, a mixed blessing. As Brader (1982) points out, for subsistence farmers, the costs of applying insecticide to a field exceeds the marginal value of the improved yields. Very little support is available to meet the special needs of small-scale farmers who produce much of the domestic food. Thus, the political power of highly capitalized export farmers, their access to capital credit and a technology suited to their production methods all work to disconnect the small-scale, food-producing farmer from the means to improve long-term yields.

However, programs to improve basic food production will necessarily be much more complex than a simple-minded rejection of all things synthetic and industrial. Traditional cultural practices may contain important ecological attributes that contribute to sustained agricultural yields. The pressure to increase productivity should not be allowed to cause a hasty rejection of such practices (FAO, 1979a). But the rapidly changing social and market characteristics of rural societies have likely made many traditional practices maladaptive to varying degrees. "Slash

and burn” or swidden agriculture made ecological sense in an age when long, fallow periods were possible, but the various sociopolitical factors that currently control farm economies demand much more intensified land use than can generally be sustained by these traditional practices. Gliessman et al. (1981) and Gomez-Pompa (1978) provide a model example of how the strengths of traditional systems can be retained in a system that is modified to meet contemporary needs.

Traditional agricultural practices obviously were developed to meet broad needs, with the control of pests being a critical component. Diverse polycultures, crop rotation, and relatively short distances to untilled vegetation all made important contributions to the reduction of many kinds of pest losses. The relationship of traditional cropping practices to pest control has been discussed in numerous articles (e.g., Janzen, 1973; Altieri et al., 1977; Glass and Thurston, 1978; Brader, 1979; Carroll, 1979; Risch, 1980; Gliessman, 1981).

In past decades, chemical-control programs have supplanted cultural-control programs for pest problems in both developing and industrialized countries. A growing disenchantment in recent years with chemical control programs, largely because of rising costs and declining long-term effectiveness, has led to a resurgence in “systems approaches” to pest control, generally referred to as Integrated Pest Management (IPM) or Integrated Pest Control (IPC). As Getz and Gutierrez (1982) point out, the emphasis in these approaches is on the compatible integration of chemical, cultural, and biological control practices in specific ecological, sociological, and environmental settings. IPC programs, involving cultural practices and the use of biological control agents, have had important successes in tropical countries, mainly with cotton (Brader, 1977) and tree crops (Majer, 1982). With the exceptions of rice (De Datta, 1980; Ku et al., 1980; Litsinger and others, 1980), and to a lesser extent, maize (Bottrell, 1979; Huis, 1981) and sorghum (Food and Agriculture Organization [FAO], 1979b), IPC programs have had virtually no impact on small-scale farmers who produce basic foods for domestic consumption. Because IPC generally emphasizes management techniques over purchased inputs, it would seem suitable for cash-poor farmers. In fact, until national priorities favor the development of region-wide IPC programs, the individual small farmer will be the one to implement such programs. So, IPC programs need to be developed that are suitable for individual farms, usually no more than a few hectares in extent, that exist in an uncontrolled matrix of farm and fallow vegetation. The success of such programs will greatly facilitate the future acceptance and development of region-wide IPC programs such as have been developed for cotton growers (Adkisson et al., 1982).

Often, the process of technology transfer is done backward. A technology is developed, and then an effort is made to get people to change their ways to accept the technological “advance.” It would seem more

logical to begin with a detailed understanding of a farmer's motivations and needs, and then begin development of a culture-specific, appropriate technology. Frequently, IPC programs are predicated on a rather simple cost-benefit analysis and consider little else beyond the pest/crop interaction. Minimizing costs usually focuses on reducing purchased crop supports and land expenses by changing the mix of fertilizers, pesticides, biological control agents, seeds, tillage, etc. Benefits are narrowly defined as decreasing crop harvest losses. Little attention is paid to reducing fluctuations in yields or to the long-term sustainability of yields, although the former decreases credit risks, and the latter decreases the ecological degradation of farmland. Also "opportunity costs" are frequently ignored, although these are of major importance to farmers. The IPC then must specifically consider minimizing conflict with such "opportunities" as wage employment, culturally desirable crop mixes, technology, and, not least, leisure time.

The long-term development of appropriate, local IPC programs must derive from an understanding of the farm agroecosystem in relationship to farm sociology and economics. From a variety of studies, some important generalizations about small-scale, tropical farms can be made. Farmers frequently need and almost always desire opportunistic wage labor. Time becomes a scarce resource, with wage-labor time competing with farm-production time. Because weed control is a major, time-consuming activity and an important factor in reducing crop yields, farmers perceive weed control as a necessary, onerous task (Holm et al., 1977). Under intensive land use in lowland, annual cropping systems, grasses and sedges become the major competitors with crops. Thus, focusing IPC efforts on the control of grass and sedge weeds reduces the opportunity costs of wage labor. At the level of individual small farms, stochastic processes become important, and small populations of pests and their predators/parasitoids may become locally extinct. IPC programs that rely on the use of native or imported predators/parasitoids with highly restrictive host lists may simply increase the variance in year-to-year crop yields as pest populations resurge and place the farmer in a position of increased debt liability. Thus, appropriate IPC programs would emphasize native generalist predator/parasitoids, especially those that have frequency-dependent, switching behavior that allows them to concentrate on the currently most common pests. Because ants are one of the more common generalist predator/parasitoids, the next section will focus on the potential impacts of ant management for small farm systems.

3.3 Advantages and Limitations of Ants in Annual Agroecosystems

3.3.1 Impact on Soil

The nesting and foraging activities of ants influence soil formation and soil/plant relations in several important ways. Although most work has

been conducted in nonagricultural temperate systems, there are good reasons for inferring an even more important role for ants in lowland tropical habitats. Ants abound throughout the lowland tropics and may affect many tropical conditions. In wet tropical regions, high rainfall can cause rapid leaching of soil nutrients, and year-long high temperatures increase average respiration rates in the decomposer community that can lead to rapid carbon losses. Finally, soil structure in the tropics does not benefit from the aerating and infiltrating processes that accompany winter freeze/thaw cycles of temperate regions. For these reasons, the activities of ants that mix soil horizons, concentrate nutrients, and aerate the soil are especially important in lowland, tropical regions (Carroll and Risch, 1983).

There is good evidence that ants are major agents in the process of soil formation (Lyford, 1963). All burrowing soil invertebrates are likely to improve the physical properties of soil by increasing its crumb structure or "tilth". Ants have less potential in this regard than earthworms, because ants do not secrete significant amounts of polysaccharides that act as important binding agents for soil particles (Barley, 1961). Bulk density of soil is further decreased around ant nests due to a concentration of organic material (Cluskey, 1981; Zacharov and others, 1981; Brieze, 1982). Infiltration and aeration, especially in heavy clay soils, is greatly improved by the many burrows and galleries of soil invertebrates (Green and Askew, 1965). Nutrients, especially carbon, phosphorus, potassium and nitrogen, are frequently significantly increased in the vicinity of ant nests (Czerwinski et al., 1969; Petal and others, 1970; Breckle, 1971; Gentry and Stiritz, 1972; Pokarzhevskij, 1981; Zacharov and others, 1981; Brieze, 1982). However, much variation exists among species. For example, Dlussky (1981) found that relative concentrations of carbon increased around the nests of *Lasius niger* but decreased around the nests of *Lasius flavus*. In general then, the activities of ants would seem to create a distribution of soil microsites that are enriched in plant nutrients and improved in structure for root penetration, aeration, and infiltration. Through their activity in the soil, ants may influence plant productivity.

3.3.2 Impact on Vegetation

Ants can directly damage plants by cutting into the soft tissue of leaves, shoot tips, buds, and germinating seeds. The leaf and bud-harvesting behavior of the attine ants is well known to neotropical farmers, and in some lowland regions, results in major crop damage (Weber, 1972; Fowler and Robinson, 1977). The economic importance of leaf-cutting ants in commercial agriculture has been reviewed by Cherrett (1986). Other ants may occasionally damage plants as well. In Trinidad, *Azteca paraensis* causes considerable damage by chewing the apical shoots of cocoa, resulting in defoliation and a change in the growth form of the tree (En-

twistle, 1972). Several species of *Crematogaster* and *Camponotus* also directly damage coffee and cocoa plants (Krantz et al., 1977). Fire ants, *Solenopsis* spp., damage germinating seeds and young seedlings of several crop plants, but Lofgren et al. (1975), suggest that this happens when alternate food sources for the ants have disappeared. In Australia, ants in the genera *Pheidole* and *Aphenogaster* influence pasture vegetation; the former by harvesting newly sown seed, and the latter by facilitating the invasion of deeply rooted plants, under conditions of overgrazing by cattle (Saunders, 1967; Johns and Greenup, 1976).

Some studies in natural communities suggest that ants may influence vegetation patterns. Brown et al. (1979) have shown that the abundance of the desert winter annual, *Filago californica*, is reduced by seed harvesting ants and, in the presence of ants, plant diversity increases in these communities (Inouye and others, 1980). Seed-harvesting behavior often results in seed dispersal, and therefore does not always have a negative effect on a plant's reproductive success. Ant dispersal of desert *Datura discolor* seeds lowers later harvesting by rodents (O'Dowd and Hay, 1980). In mesic West Virginia forests, Heithaus (1981) has shown for several plant species that dispersal by ants lowers both pre- and post-dispersal seed depredation by rodents.

With the exception of miscellaneous reports concerning the role of seed-harvesting ants on small-grain agriculture, the impact of seed-harvesting ants in agroecosystems has largely been ignored. The role of seed-eating ants in crop/weed interactions has considerable potential for several reasons. (1) Many weed seeds are small and therefore easily transported by ants. (2) The process of cultivation creates conditions suited to colonization by weed seeds from the soil bank and from dispersal. During early phases of cultivation, following land clearing, production of new seeds is relatively low; therefore, seed-eating ants may effectively lower the first generation population of weeds. (3) The clearing of fallow vegetation in preparation for planting temporarily eliminates or reduces some alternative foods, such as plant exudates and herbivorous insects. Because many seed-eating ants are also opportunistic insect predators and scavengers, the reduction of their food supply may force an increased concentration on seed harvesting. This assumes, of course, that the populations of seed-eating ants are not, themselves, also greatly reduced by the cultivation and burning practices. (4) Perhaps more than in later successional stages, a high percentage of agricultural weed species produce large numbers of seeds that have poorly developed chemical defenses. The impact of generalist seed-eating ants could strongly modify the plant community in favor of more chemically protected species. This would probably favor dicots over grasses and influence density-dependent competitive interactions between annual grasses and dicots. This has considerable agricultural significance, because four of the ten most serious weeds, on a worldwide basis, are annual grasses (Holm et al. 1977). In

general, grass weeds are extremely difficult to control in the mixed cropping systems practiced by small farmers in the tropics.

In moist, lowland, neotropical agroecosystems, *Solenopsis geminata* harvests large numbers of small seeds and frequently damages newly planted corn seed. In southeastern Mexico, we found that *S. geminata* had harvesting preferences among seeds of similar size, generally preferring grasses over dicots and sedges. We also found that *S. geminata* would remove more than 95% of experimentally sown seeds of the grass *Paspalum conjugatum* (Carroll and Risch, 1984). Also, in Puerto Rico, *S. geminata* collects large numbers of the seeds of the important grass weed, *Chloris radiata* (Torres, 1981). The observation that seed-harvesting ants can remove large numbers of weed seeds suggests that these ants may have a useful role in weed-control practices and that their behavior may contribute to the outcome of competitive interactions among weed species (Risch and Carroll, 1986).

Many crops (e.g., corn) have symbiotic associations with vesicular-arbuscular mycorrhizal (VAM) fungi, such as *Glomus* spp. Because the spores and sporocarps of VAM fungi are large, often similar in size to insect eggs, and because they will be concentrated in the rhizosphere where many ants construct their nests, it is important to know if any ants forage for these fungal spores. If ants forage for the fungal spores and destroy them, it is possible that this activity may slow the development of the mycorrhizal/crop association in newly planted fields. On the other hand, McIlveen and Cole (1976) and Hoffman and Carroll (unpublished) found large concentrations of VAM fungi in ant nests, and the suggestion that ants may disperse viable spores has intriguing potential for improving mycorrhizal establishment in fields.

The presence of aggressive ants in flowers may reduce visits by pollinators and thereby lower fruit and seed production. For example, in southern Mexico, the presence of *Solenopsis geminata* workers in female squash flowers (*Cucurbita moschata*) prevents visits by generalist pollinators, such as *Bombus* spp., but does not inhibit the specialist squash pollinators, such as *Peponapis* spp. (C. Hoffman, pers. comm.). Such occurrences, however, appear uncommon. Curiously, the presence of the aggressive ant *Azteca chartifex* is said to improve the pollination rate of cocoa by ceratopogonid midges (Vellow, 1971), but the evidence is unclear.

3.3.3 Impact on Arthropod Pests

Ants may limit arthropod populations in their role as predators, or may aid arthropod populations in their role as mutualists. The importance of ants as predators or mutualists with other arthropods is best known for tree populations and forests. Some examples include the control of pests in temperate forests (Dmitrienko, 1964, Dobrechau, 1964; Malysheva,

1964; Adlung, 1966; Finnegan, 1975; Kim and Murakami, 1980; Laine and Niemla, 1980). Ants have also been used to control pests in tropical and sub-tropical tree plantations, for example, plantations of citrus and date palms (DeBach, 1974), bananas (Torres, 1982), and coconuts and cocoa (Leston, 1973; Room, 1973; Majer, 1982).

The mutualism between many species of ants and homopterans is well known (e.g., Way, 1963), but the consequences of these interactions for the host plant of the homopterans are not obvious. Homoptera are a mixed blessing from the plant's viewpoint. In some cases, the attraction of aggressive and/or predatory ants that results from the presence of the homopteran appears to confer a net advantage to the plant; that is, the production loss from the homopterans plus other herbivores is less than the loss that would result from the total herbivory in the absence of ants (Wellenstein, 1953; Gosswald, 1954, 1958; Stapley, 1971; Leston, 1973; Majer, 1974; Bentley, 1977). Other examples cite net negative effects for the plant (DeBach, 1974; Taylor and Adeoyin, 1978).

In the southern United States, ants are important predators in soybean fields (Whitcomb et al., 1972), sugar cane fields, and unsprayed cotton fields (Battenfield, 1982). Because most commercial, annual crops are intensively treated with pesticides in the southern United States, the biological control potential for ants is essentially unknown, and probably not able to achieve its full potential.

The impact of ants on arthropod populations in tropical, annual cropping systems has not received much attention beyond various anecdotal remarks that they must be important because they are so abundant. Field experiments in southeastern Mexico have demonstrated that *Solenopsis geminata* is an efficient scavenger in milpas (Saks and Carroll, 1980; Risch and Carroll, 1982a), and can significantly reduce pests on corn and squash (Risch and Carroll, 1982b). In Costa Rica, *S. geminata* and other ants are important predators on the eggs of corn rootworms *Diabrotica* spp. (Risch, 1980). Perfecto (1989) has shown through a series of field experiments that ants, principally *Solenopsis geminata*, *Ectatomma ruidum* and *Pheidole radowszkoskii*, can reduce *Spodoptera frugiperda* and *Dalbulus maidis* in traditional rain-fed corn milpa systems in Nicaragua. She found a similar, though somewhat weaker, result in nearby commercial irrigated corn fields where ant activity was lower, presumably due to higher applications of insecticides and greater soil disturbance from mechanical tillage.

Ants are density-responsive predators and can therefore concentrate on localized pest populations. The pheromone recruitment behavior of most ants makes the density-responsive component of foraging very efficient relative to that of solitary foragers. The critical question, however, is how large and concentrated the patch of food must be before significant recruitment of other workers will occur. Other factors being equal, pests that oviposit unprotected egg masses or have group-feeding larvae may

be more subject to density-responsive predation by ants than are those pests that lay dispersed eggs and have dispersed larvae. Thus, the size and patch density of pests in the agroecosystem are likely to have important consequences on their depredation rates by ants.

Aggressive species of ants deter pest feeding, even pests that are too large to be successfully captured, and thereby have an ecological role beyond that achieved by satisfying colony food needs (Janzen, 1966; Bentley, 1977). This behavior may be particularly important for plant-sucking insects that require a substantial amount of time to penetrate and locate the appropriate host tissue and harvest sufficient amounts of nitrogen-dilute sap (Way, 1954; Auclair, 1963). This behavior may also have a negative impact if it encourages the movement of insects acting as vectors of plant pathogens. Also, those species of pest homopterans that are tended by ants for their honeydew secretions may achieve longer periods of uninterrupted feeding because the ants ward off predators and/or construct shelters for the homopterans (Way, 1963).

3.4 Ecological Aspects of Ants and Management Questions

Improvements in the use of any beneficial organism in an agroecosystem will depend on the extent to which ecological characteristics of the organism may be manipulated to achieve management goals. In the following section we discuss some key ecological characteristics of ants; some of which contribute to management goals while a few may limit the use of ants in the management of an agroecosystem.

1. Colony growth rates and population increases of ants may be too slow to respond to rapid increases in pest population density. This may be especially true in the first planting season, when land clearing and burning practices severely disrupt the resident ant fauna. In general, we would expect a light fire to eliminate surface, litter-nesting species, such as *Odontomachus* spp., but not to have much direct effect on species that nest underground. In fact, light surface fires may result in at least temporarily large increases in populations of ground-nesting species. For example, the frequency of nests of the ground-nesting ant *Ectatomma tuberculatum* in Costa Rica increased twofold following a fire (Carroll, 1974). It is unclear how a temporary increase in population/colony densities of ground-nesting ant species or a changed harvest rate of prey will influence agroecosystems. In our preliminary study, an increase in ant foraging activity in old polycultures suggests that some effect from clearing practices may occur. The reason why ant communities have not been adequately studied in tropical agroecosystems, other than tree crop systems, is probably a consequence of the untested assumption that the devel-

opment of an efficiently foraging ant community requires more time than is available in annual or biannual cultivation (for example, see Leston, 1973). Although this assumption may be true for some cropping systems, our observations lead us to believe that ant faunas develop rapidly in the traditional systems of the lowland neotropics.

2. The location of crops changes frequently, but many ant colonies have fixed nest sites. Shifting cultivation practices no doubt prevent ant communities from achieving equilibrium species frequencies, but this has little to do with the likelihood that ant communities will significantly influence the development of pest complexes within a crop. In the early colonization period in a recently planted field, there may be a large number of colonizing ant species. As territorial species become established, the total number of ant species within a field may decline. Thus, changes in species composition and frequencies, and changes in the density of ant foragers over time will undoubtedly have important consequences for the development of trophic guilds.
3. The recruitment behavior of many ant species make them classic examples of density responsive predators and scavengers. This behavior is probably beneficial because ant foragers may concentrate on foci of pest populations, but there may be negative aspects as well. Scavenging ants may harvest synthetic food that is intended to support beneficial predators such as lacewings (Chrysopidae). In management schemes to maintain parasitoid populations, the predation pressure from ants on the neutral alternate host for the parasitoids could have important negative consequences on the parasitoid population (Carroll, 1978). This is especially true in cases where parasitized hosts are preferentially taken as prey by ants. For example, black, parasitized corn leaf aphids are often removed from populations of healthy aphids by minor workers of *Solenopsis geminata* (Carroll, unpublished field notes; see also DeBach, 1974). To the extent that ants are density-responsive predators, we would predict that, other factors being equal, ant foraging would have a stronger effect on pest species that have clumped distributions than on pest species that have highly dispersed populations.
4. Some ants have aggressive reactions to colony disturbance and thereby interfere with agricultural work. The Old World tailor ant *Oecophylla* and the New World members of the *Solenopsis* fire ant complex are often annoying to field workers in this manner (Lofgren et al. 1975; Kranz et al. 1977).
5. Territorial species of ants may lower the overall harvest rate of pests by excluding other ant species from their territories. The occurrence of ant "mosaics," nonoverlapping territories of dominant species, is now firmly established and probably a general "rule" for ant species distributions in the tropics (Leston, 1978). As Leston (1973) points out, many of these dominant species are very efficient predators, and

some ant species are able to coexist within the territories of dominant species. In annual and biannual cropping regimes, the frequent disturbance of the habitat may prevent somewhat the development of exclusive territories, but this point clearly needs investigation.

6. Ants are common and do not have to be imported. The number of ant species in small agricultural fields and plantations is often large. Leston (1973) remarks that about 300 ant species occur in the forested parts of Ghana and "... can for the most part, be found in cocoa." Room (1975) found similar total numbers of ant species in the following habitats in New Guinea: forests (138 species), rubber plantations (121 species), cocoa plantations (119 and 131 species), coffee plantations (99 species), oilpalm plantations (92 species), grassland (177 species), savanna (158 species), and urban grasslands (105 species). It is particularly interesting that the stable, multidimensional forest habitat had a total ant fauna (138 species) similar to that of the structureless and shifting urban grassland (105 species). Very little is known about the number of ant species that occur in annual or biannual cultivation. In Florida, Whitcomb and others (1972) found fifty ant species in soybean fields, and we would expect much larger numbers for tropical polycultures.
7. Ants may be cheap to maintain in agroecosystems because adult workers can be fed largely on sugar sources. In fact, the proventricular constriction in the adults of many species prevents their eating any solid food other than very small particles (Wheeler, 1910; Eisner, 1957; Eisner and Happ, 1962; Wilson, 1971).
8. Colony foraging behavior may be manipulated. For example, sugar sources, such as plants with extrafloral nectaries, crushed sugar cane, etc., may be used to attract ant foragers to particular parts of the field or parts of the crop plant that are especially vulnerable to pest damage (Leston, 1973). In a more general sense, the use of sugar sources may increase the average foraging time and distance of foragers searching for protein food to supply developing larvae (Carroll and Janzen, 1973). Thus, providing a source of sugar for foraging adults not only supplies them with a needed source of calories for increased foraging activity, but may also encourage them to capture pest insects as sources of fat and protein for the larvae.
9. Ants are capable of storing food and therefore have a higher food saturation curve than simple colony biomass would suggest. Although storage of dead insects as food does occur, particularly in semi-arid regions or during drier parts of the year, the most important storage items are seeds gathered by granivorous species. Increased food stores increases the reproductive rates, but little is known about the exact lag time before reproductive rates begin to rise, and how great such increases in reproduction may become. In other words, we need to know the properties of the economic demand function

for the colony as its food supply changes. This relationship is unknown, in detail, for any ant species. However, Oster and Wilson (1978) have made an important contribution to our understanding of the evolutionary factors that modify colony caste/ant/task composition as a function of the kinds and frequency of contingencies that colonies experience.

10. It is known that ants are capable of regulating, in a facultative sense, their colony size in response to food levels. When food levels are low, cannibalism of the colony brood increases, reproductive rates decrease, and the colony worker density decreases at a slow rate (Brian, 1965; Markin, 1970; Wilson, 1971). When food levels are high, the reverse happens, and colony size increases. Thus, the brood of the colony, as an emergency reserve, acts as a homeostatic mechanism to dampen the effects of a fluctuating food supply on the worker force (Carroll, 1974).

This colony response to varying food levels means that (i) more than other predators, ants will dampen the effects of a fluctuating food supply; and (ii) they may persist in an active state during the nongrowing season and thereby respond rapidly to the buildup of pest populations during the early part of the growing season. Many other predators would have to come out of a developmental or reproductive diapause before their populations could begin to increase in response to an increase in pest numbers.

Ant larvae should be ideal food storage devices, because they should have low maintenance costs, put little resource into inedible cuticular structure, can contain large fat bodies, and have long starvation times (Janzen, 1967; Carroll and Janzen, 1973). Eggs produced by workers and then fed to queens and larvae are known from many diverse groups of ants (LeMasne, 1953; Freeland, 1958; Brian, 1965; Markin, 1970; Weber, 1972). Pharyngeal proteinaceous secretions are also produced by the workers and fed to the queens (Naarman, 1963). Although such eggs and secretions may well be simply part of the colony's catabolic pathways, they also may be indicative of complex mechanisms regulating the flow of food reserves within the colony.

11. The species mix of the ant community can be manipulated through selective poisoning or supplemental feeding. For example, species with small-sized workers (e.g., *Monomorium*) may be eliminated from a field by using toxic baits in containers that have very small openings. Some foods are attractive to particular species; for example, linoleic and linolenic acids are phagostimulants for imported fire ants (Lofgren et al. 1975). Thus, it may be possible to modify the species composition in agroecosystems by using baits containing phagostimulant. This could, of course, be used with poison baits to eliminate undesirable species or phagostimulants could be used in supplemental feeding schemes to increase the density of desirable species.

12. Some kinds of ants can be easily moved with subsequent minimal emigration. For example, because *Solenopsis geminata* does not occur in heavy, fallow vegetation, small colonies of *S. geminata* may be moved into a new polycultural planting with little likelihood that they would escape into surrounding second-growth vegetation. A knowledge of the nesting requirements of desirable and undesirable ant species is, of course, a prerequisite for any scheme to manipulate the ant fauna by moving colonies. Colonies of European wood ants (*Formica* spp.) are routinely moved as part of pest management schemes in European forests (Anon., 1965), so that in principle, such practices may be possible in tropical agroecosystems. The above examples show that much needs to be done before ants can be used effectively as part of an IPC program. Still, what we do know points to the use of ants as a beneficial and economical component of an IPC program. (Carroll and Risch, 1983).

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4. Cropping Systems, Insect Movement, and the Spread of Insect-Transmitted Diseases in Crops

Alison G. Power

4.1 Introduction

Food production in the tropics has undergone tremendous modification in the last several decades, with traditional small, diversified farming systems being replaced by large-scale, input-intensive monocultures. It is clear that insecticide abuse and widespread dependence on single crop genotypes have resulted in many problems for the farmer, the environment, and the health and safety of rural workers (Bull, 1982). Along with other insect pests, insects that transmit pathogens to crops have evolved resistance to widely-used insecticides and have escaped regulation by their natural enemies. It is essential that we use our understanding of basic ecological processes to address the need for low-input agricultural technology for the tropics. If we are to encourage decreased use of pesticides, then we must offer alternative solutions to the problems of pest damage. These solutions depend on an adequate understanding of pest biology and behavior.

The goal is to manipulate pest organisms to decrease the damage they cause. One of most direct methods of control is the alteration of the crop itself, through plant breeding or through planting arrangement. Unfortunately, varieties resistant to insect vectors are not available for many crops. Moreover, as new resistant varieties have been developed, vectors (like other insect pests) have evolved to overcome resistance traits in the plants (Pathak and Heinrichs, 1982). Where resistant varieties exist, it is

important to deploy them in a manner that slows the process of pest evolution to overcome resistance (Gould, 1983).

One of the most effective methods of reducing the abundance of insect vectors is manipulating the cropping system. Because insecticides often do not kill vectors in time to prevent the spread of pathogens, methods of cultural control are particularly appropriate for the control of this type of insect pest. Both the ecological and the agricultural literature are full of examples of the effects of plant spacing and plant diversity on populations of herbivorous insects, including vectors. Few of these studies, however, investigate the mechanism of pest response to these factors. There is ample evidence that small-scale, diversified farming systems tend to have fewer pest problems than the modern monocultural systems that are becoming dominant in the tropics. But our understanding of why these systems work is far from complete. What factors in the cropping pattern are actually responsible for the effect? What characteristics of the host plant or the surrounding vegetation do insects respond to? What is the mechanism of that response? If we find lower pest abundance, is it due to decreased colonization, decreased reproduction, increased emigration, or increased mortality? The role of insect ecology is to help us identify the mechanisms of insect response, so that we can design new systems that effectively manipulate that response.

This discussion will focus on some promising methods of cultural pest control for vector insects, methods based on natural systems and indigenous farming systems that depend on the manipulation of planting design. I will illustrate these ideas by describing my own research on a leafhopper vector in maize cropping systems. After first examining the major processes that drive the epidemiology of insect-transmitted diseases, I will consider the influence of several characteristics of cropping systems: the number of plant species present, the density of those plants, and the quality of the host plant as food for vector insects. Changes in the quality of the host plants or the background vegetation may influence the foraging behavior of the vector, leading to changes in disease incidence.

4.2 Insect-Borne Pathogens of Crop Plants

4.2.1 Pathogen Transmission Systems

Plant pathogens transmitted by insects cause significant yield losses in crops throughout the tropics. More than 90% of insect-borne pathogens are spread by homopteran insects; of these, approximately 60% are transmitted by aphids and 25% by leafhoppers and planthoppers (Eastop, 1977). Most of these pathogens are viruses, but various mycoplasma-like

organisms (MLOs), spiroplasmas, and bacteria are also transmitted by aphids and leafhoppers.

The characteristics of the transmission system strongly influence the epidemiology of a plant disease. Pathogens transmitted by insects are commonly classified as persistent, semipersistent, or nonpersistent, based on how long the pathogen is retained in the insect (Watson and Roberts, 1939). Nonpersistent pathogens are retained for minutes to hours, semipersistent pathogens for hours to days, and persistent pathogens for weeks to vector lifespan. One hundred percent of the leafhopper-borne pathogens are persistent or semipersistent, whereas only 30% of the aphid-borne pathogens are of these types (Eastop, 1977). Leafhoppers are not known to transmit nonpersistent pathogens.

This difference in the common transmission mode for these two groups of vectors apparently reflects differences in feeding behavior. Aphids exhibit a characteristic “host-testing” probing behavior, during which the stylets enter the epidermal cells of the plant before beginning a deeper feeding probe, where the stylets are inserted intercellularly to the phloem (Harris, 1977). It is primarily during these “tasting” probes that nonpersistent pathogens are transmitted. Leafhoppers do not exhibit this superficial probing behavior before beginning a feeding probe, and therefore would not be particularly effective vectors of nonpersistent pathogens.

Persistent and nonpersistent transmission systems differ in several ways in addition to the average pathogen retention time by the insect vector. The feeding period required for the insect to acquire the pathogen from a diseased plant or transmit it to a healthy plant is quite short for nonpersistent pathogens, on the order of 15 to 60 seconds, and longer for persistent pathogens, ranging from several hours to several days (Figure 4.1). Once an insect acquires a persistent pathogen, the pathogen becomes circulative and can be carried by the insect for long periods, whether or not a new source of inoculum is encountered. This period may be the entire lifetime of the insect, particularly if the pathogen multiplies within its host. In contrast, a nonpersistent pathogen is lost within minutes or hours of acquisition if a potential host is not encountered.

After an insect has acquired a persistent pathogen, a latent period of incubation is required before the pathogen can be transmitted to a plant. In both kinds of transmission systems, a latent period occurs in the infected plant before a noninfected insect can acquire the disease from it. For persistent pathogens with latent periods that are long, relative to the life of the plant (as is the case for many annual plants), the probability is low that a host plant that acquired the disease early in the season can act as a source of inoculum for other host plants in the same field during that growing season. In this type of transmission system, the major source of inoculum will be colonizing infective insects from outside the field. The dynamics of disease spread in such a system is called monocyclic

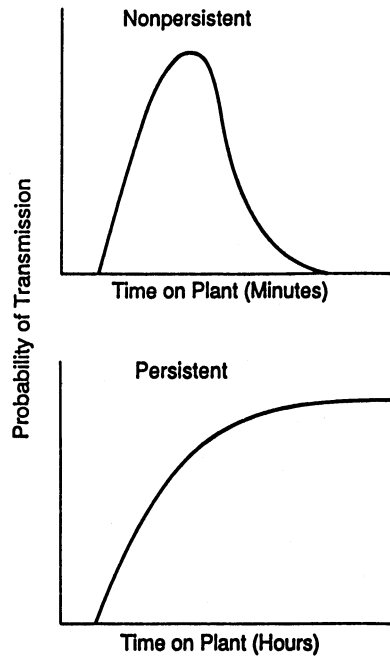


Figure 4.1. The probability of transmission of persistent and nonpersistent pathogens as a function of the time an insect feeds on a plant.

(Thresh, 1983), because the source of inoculum does not increase within the crop during the course of single growing season (Figure 4.2). On the other hand, when latent periods are short relative to the life of the plant, as they are in perennial crops (e.g., grapes, tree crops), secondary sources of inoculum may develop within the crop. In this case, persistent diseases may be polycyclic (Thresh, 1983), spreading from sources of inoculum that multiply as increasing numbers of plants become infected (Figure 4.2).

Because the pathogen does not become circulative in nonpersistent transmission systems, no latent period is necessary before the insect can transmit the disease. When the incubation period in the plant is also relatively short, new sources of inoculum develop very quickly, and secondary spread within a field is high. Although nonpersistent pathogens tend to spread in a polycyclic way, they may show monocyclic spread if infective insects do not stay to breed on the crop.

4.2.2 Vector Movement and Pathogen Spread

For a persistent pathogen, the number of plants that a vector can infect depends on the average time the insect feeds on a plant, the number of plants it feeds on, and the feeding period required to transmit the path-

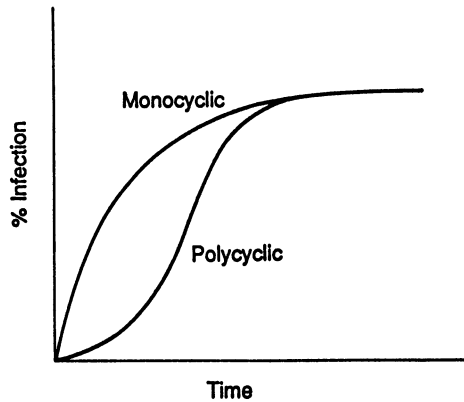


Figure 4.2. The spread of infection in a plant community as a function of time. In monocyclic spread, the source of inoculum does not increase within the crop during the course of a single growing season, whereas in polycyclic spread, the sources of inoculum multiply.

ogen. The number of plants infected per vector per unit time is therefore the product of the probability of transmission per plant visit and the number of uninfected plants visited per unit time. We have seen that the probability of transmission is a monotonically increasing function of the time spent feeding on a plant (Figure 4.1). Given an unlimited pool of uninfected plants and a limited time period available for infecting plants (potentially the lifetime of the insect), the number of plants visited per vector may be represented by a negative exponential function of the time on a plant plus the time spent searching for a plant (Figure 4.3). The

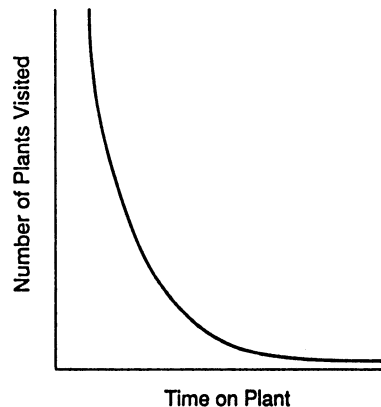


Figure 4.3. The number of plants visited by an herbivorous insect within a given period of time, as a function of the average time the insect feeds on a plant.

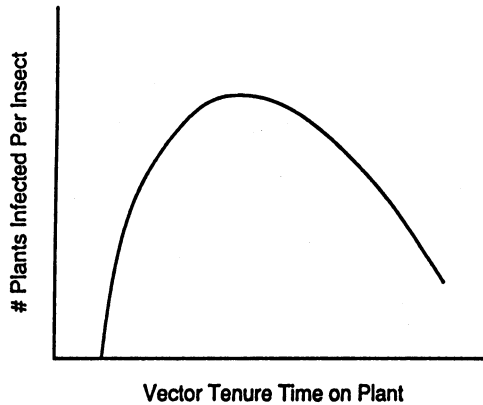


Figure 4.4. The number of plants infected by a single vector as a function of the average time the insect feeds on a plant.

time spent on each plant (residence time) is thus inversely related to the rate of movement.

By combining the transmission function for a persistent pathogen (Figure 4.1) with the plant encounter rate (Figure 4.3), we arrive at a function relating the time a vector spends on the plant to the disease incidence. In graphical form, we see that the highest infection rate results when the insect remains on each plant for a period equal to that required for pathogen transmission (Figure 4.4). If the insect remains on each plant for less than this period, it contacts more plants but is less likely to transmit the pathogen to any plant. On the other hand, if the insect remains on each plant for longer than the optimal inoculation period, it has a high probability of transmitting the pathogen to each contacted plant, but it contacts fewer plants. Note that this relationship depends on the shape of the transmission function and therefore holds only for persistent pathogens. For a more complete treatment of this relationship, see Power (1985).

In a persistent pathogen system where the probability of secondary spread is low, the rate of infection of plants will depend simply on the required transmission time and the average time an insect feeds on a plant (Figure 4.4). The situation becomes much more complex in a non-persistent system where secondary infection is high. Here, the infection rate will depend on the time required to transmit the pathogen to an uninfected plant, the time required to acquire the pathogen from an infected plant, the length of time the insect retains the pathogen, the incubation period in the plant, the proportion of infected and uninfected plants, and the average time an insect feeds on an infected or uninfected plant. In this case, we must take into account the probability of transmitting the pathogen to an uninfected plant as a function of time spent

feeding, the probability of acquiring it from an infected plant as a function of time spent feeding, the probability of still having the disease as a function of time spent searching, the average time an insect feeds on a plant, the average time an insect spends searching for plants, and the incubation period in the plant.

We expect the highest infection rate to occur when the average time spent on an uninfected plant is equivalent to the period required for transmission, the time spent on an infected plant is equivalent to the period required for acquisition, and time spent between plants is less than the average pathogen retention period. These parameters plus the incubation period in the plant will determine the rate of spread. This second model of disease spread requires the simultaneous maximization of several functions, and thus becomes much less tractable. The relationship between insect movement and disease dynamics of nonpersistent pathogens clearly warrants the attention of theoreticians.

These conceptual models of disease transmission highlight the importance of localized plant-to-plant movement for disease incidence. Some important parameters, such as the probability of transmission as a function of feeding period, the probability of acquisition as a function of feeding period, and the incubation period in the plant are often measured in standard laboratory transmission studies. The average time spent on each plant (residence time) or rate of movement is best measured in the field, but this has rarely been done in a way that could be used to predict infection rates.

Differences in transmission systems and in the feeding behavior of aphids and leafhoppers will obviously influence the response of pathogen dynamics to changes in the cropping system. Characteristics of the host plant or the plant community that decrease the average duration of tasting or feeding probes by vectors may lead to higher rates of transmission for nonpersistent pathogens and lower rates for persistent pathogens. For example, plant communities in which herbivores move often from plant to plant could lead to low infection rates for persistent pathogens that have long transmission times, but high infection rates for nonpersistent pathogens. In the following sections I review the literature on the influence of cropping system on vector and pathogen dynamics and illustrate the importance of vector movement for disease dynamics in the corn stunt system.

4.3 The Influence of Cropping Systems

4.3.1 Plant Diversity and Intercropping

In general, insect herbivores tend to be less abundant in cropping systems of higher diversity (Andow, 1983, 1986; Risch et al., 1983), and this

pattern holds for most insect vectors. In a review of polyculture experiments, Andow (1983) reported that monophagous herbivores were more likely to decrease in diverse systems than were polyphagous ones (61.3% versus 27.1%), and less likely to increase (10.0% versus 43.8%). For homopterans insects the trend was similar: of thirty-five monophagous species of Homoptera, twenty-seven decreased with increasing vegetation diversity, and only three increased. In most of these studies, however, the influence of plant diversity was not rigorously separated from the influence of plant density or quality, which may change as plant diversity increases. For example, although Toba et al. (1977) found lower populations of alate aphids on cantaloupe intercropped with radish or swiss chard, the cantaloupes in these plots were clearly stunted.

A notable exception to this confounding of plant diversity with density and quality is the work of Farrell (1976a, b) on the aphid *Aphis craccivora*, which transmits the rosette virus to peanut. In polycultures of peanuts (*Arachis hypogaea* L.) and beans (*Phaseolus vulgaris* L.), Farrell (1976b) controlled for the effects of plant diversity, host plant density and overall plant density. His results indicate that overall plant density was of overriding importance in determining per-plant aphid abundance.

Another factor that often confounds the interpretation of comparisons between cropping systems of varying diversity is the feeding range of the herbivore. The addition of plant species that may serve as alternate host plants for an herbivore will clearly have a different effect than the addition of nonhost plants. Thus, we would expect generalist and specialist herbivores to respond differently to increasing plant diversity, such that monophagous insects, which feed on only one component of an intercropped system, should be less abundant in these systems, whereas polyphagous herbivores should be more abundant. The variable that determines herbivore abundance is the ratio of host to nonhost plants, rather than the actual number of plant species.

Experiments with leafhoppers provide an illustration of the importance of feeding range. Populations of the potato leafhopper, *Empoasca fabae*, on cantaloupe are higher when it is interplanted with other host plants (Toba et al., 1977). On the other hand, when beans (an important host plant) are interplanted with nonhost plants, the abundance of this leafhopper decreases (Andow, 1983; Lamp et al., 1984). Similarly, populations of *Empoasca kraemeri* were reduced when beans were interplanted with nonhost grasses (Altieri et al., 1977; Schoonhoven et al., 1981), but were not affected by the presence of the broadleaf weed *Amaranthus dubius* (Schoonhoven et al., 1981). The abundance of the leafhopper *Scaphytopius acutus* (Say) increased in peach orchards when the ground cover consisted of host plants, but was not affected when a nonhost grass was used (McClure et al., 1982).

If the insect vector is a relatively specialized feeder, as is the case for several of the more important leafhopper vectors, we would expect lower

vector abundance in plant communities of higher diversity. On the other hand, many of the important aphid vectors, such as the green peach aphid *Myzus persicae*, are broad generalists in their feeding habits and may be likely to increase in abundance if increasing plant diversity increases the number of potential host plants in the community. Although Horn (1981) found that *M. persicae* was less abundant in weedy plots than in weed-free plots (even when plant size was unaffected), this result could be because of the increase in overall plant density rather than the increase in plant diversity. Even for relatively oligophagous herbivores, increasing diversity may provide a greater number of suitable hosts and lead to increased abundance.

One hypothesis to explain the phenomenon of lower herbivore abundance in diverse cropping systems is that insects are confused by the odors of nonhost plants and unable to find their host plants. Chemical confusion is unlikely to be applicable to most homopteran insects, however, because aphids and leafhoppers are known to be largely unaffected by olfactory stimuli (Kennedy et al., 1959a, b; Saxena and Saxena, 1975). In a study of the sensory stimuli of *Amrasca devastans* Distant, Saxena and Saxena (1974, 1975) showed that this leafhopper was attracted by plant volatiles only up to 1 cm from the plant surface. Odors from nonhost plants are thus unlikely to reduce colonization by homopteran insects to stands of plants, but may affect discrimination behavior at a closer range.

A related hypothesis to explain lower numbers of herbivores in diverse plant communities proposes that rates of emigration rather than colonization are affected by the presence of nonhost plants. Studies of various leaf beetles indicate that they have a shorter residence time in plant patches with nonhost plants and move farther after encountering a nonhost plant (Bach, 1980a, b; Risch, 1980, 1981). In this case, gustatory cues are more likely to be important than olfactory or visual cues. Experiments show that the probing response in aphids is elicited by host and nonhost plants alike (Harris, 1977). A long feeding probe, however, is only initiated when the insect receives the correct gustatory stimuli from a host plant. For these insects, probing a nonhost plant is also likely to cause shorter residence times and longer flights (Kennedy et al., 1959a, b). Saxena and Basit (1982) found that both colonization and residence time of the leafhopper *Amrasca devastans* on a host plant were influenced by the presence of nonhost plants.

How do these responses to plant diversity affect the incidence of insect-borne diseases? If the presence of nonhost plants reduces colonization, disease should be reduced because of lower vector abundance. If, on the other hand, the presence of nonhost plants does not affect colonization but causes increased movement within a field, we might expect lower incidences of persistent diseases but higher incidences of nonpersistent diseases.

Table 4.1. Pathogens for which disease incidence is lower in more diverse cropping systems

Pathogen	Type	Vector	Reference
Alfalfa mosaic virus	N ^a	Aphid	Gibbs & Harrison, 1976
Bean common mosaic virus	N	Aphid	Van Rheen et al., 1981
Bean yellow mosaic virus	N	Aphid	Corbett & Edwardson, 1957
Beet yellows virus	P	Aphid	Hull, 1952
Cauliflower mosaic virus	N	Aphid	Broadbent, 1957
Chlorotic mottle virus	N	Aphid	Toba et al., 1977
Corn stunt Spiroplasma	P	Leafhopper	Pitre, 1969 Pitre & Boyd, 1970 Power, 1987
Cucumber mosaic virus	N	Aphid	Gibbs & Harrison, 1976
Peanut rosette virus	P	Aphid	Farrell, 1976b
Pepper veinbanding mosaic virus	N	Aphid	Simons, 1957
Tomato yellow leaf curl virus	P	Whitefly	Al-Musa, 1982
Turnip mosaic virus	N	Aphid	Broadbent, 1957

^a Type of pathogen transmission system is given as P (persistent) or N (nonpersistent).

In fact, disease incidence tends to be lower in diverse systems for both persistent and nonpersistent diseases (Table 4.1). The explanation may be the indiscriminate alighting and probing response of aphids to nonhost plants. Because aphids alight in response to visual cues that do not allow them to distinguish between host and nonhost plants, they land on nonhost plants and probe superficially before rejecting the plant (Harris, 1977). Nonpersistent pathogens are not retained beyond this initial probing, and thus vectors can lose nonpersistent pathogens to plants that are not hosts of the pathogen. Because plant species that are hosts of the insect vector are not necessarily suitable hosts of the pathogen, a similar process may occur in cases where two host plants of the insect are intercropped. In these systems, polyphagous insects alight and feed on all plants, acquiring the pathogen from infected plants of one species and losing it when feeding on the other species. If the insect is preferentially attracted to the added crop, this second species may act as a "trap crop" for both the vector and the pathogen (Farrell, 1976b; Al-Musa, 1982). Toba et al. (1977) define a "protection crop" as the inclusion of noncrop plants that provide feeding sites for infectious insects, but are not susceptible to the pathogen or suitable for insect reproduction. This method of intercropping or barrier cropping has led to lower disease incidences of nonpersistent pathogens in several crops (Jenkinson, 1955; Broadbent, 1969).

Clearly, if more diverse cropping systems contain additional hosts of both the vector and the pathogen, disease incidence is likely to be higher. Several programs for disease control in agricultural systems are based on the eradication of alternate hosts of the pathogen. For example, the spread of beet curly-top virus has been controlled in many areas by eradicating Russian thistle, the alternate host of both the virus and the leafhopper vector (Gibson and Fallini, 1963). Even in these systems, however, higher diversity does not always result in increased disease spread. The increase in disease incidence due to more hosts may be balanced by other changes that tend to reduce vector colonization, such as increased plant density. In a comparison of conventional tillage and no-tillage in corn, All et al. (1977) found that Johnsongrass (*Sorghum halepense*), an alternate host of the maize dwarf mosaic and maize chlorotic dwarf viruses, was significantly more abundant in the no-tillage system. This did not result in higher disease incidence, however, because the most important vector, the leafhopper *Graminella nigrifrons*, was less abundant in this system.

4.3.2 Planting Density

Although dense stands of host plants often have higher populations of herbivorous beetles than sparse stands (Root, 1973; Kareiva, 1983), the opposite tends to be true for homopteran insects. The abundance of most aphids and leafhoppers decreases with increasing plant density (A'Brook 1964, 1968, 1973; Mayse, 1978; Halbert and Irwin, 1981; Johnstone et al., 1982; Power, 1987). In some cases, insect abundance per plant is lower in dense stands but absolute numbers of insects (per unit area) are higher. This probably indicates that the pool of potential colonists is limited, so that as host density increases, the number of insects per plant is diluted over an increasingly large number of plants. In many cases, however, absolute numbers of insects are lower in dense stands, suggesting a behavioral response to density, such that colonization to dense stands is reduced.

For both aphids and leafhoppers, the amount of bare ground present in a plant community can influence abundance (Smith, 1969, 1976; Schoonhoven et al., 1981). These insects appear to be attracted to the visual contrast provided by the green host plant against a dark background (Kennedy et al., 1961). Higher plant density obscures this contrast and may be less attractive to colonizing insects. The difference between the response of homopteran insects and the response of other herbivores, such as chrysomelid beetles or lepidoptera larvae, may be a result of the use of different foraging cues. If these chewing herbivores tend to use chemical cues rather than visual ones, they may be more likely to increase in dense stands (Stanton, 1983).

The reduced abundance of aphids and leafhoppers in dense stands is typically mirrored in a lower incidence of insect-transmitted disease (Ta-

Table 4.2. Pathogens for which disease incidence is lower at higher planting densities

Pathogen	Type	Vector	Reference
Barley yellow dwarf virus	P ^a	Aphid	Slykhuis et al., 1960
Beet yellows virus	P	Aphid	Blencowe & Tinsley, 1951 Heathcote, 1970, 1974 Johnstone et al., 1982
Corn stunt spiroplasma	P	Leafhopper	Power, 1987
Peanut rosette virus	P	Aphid	Booker, 1963 Hull, 1964 A'Brook, 1964, 1968 Davies, 1976 Farrell, 1976a, b
Pea leaf-roll virus	P	Aphid	Way & Heathcote, 1966
Sugarbeet mosaic virus	N	Aphid	Blencowe & Tinsley, 1951
Tomato curly-top virus	P	Leafhopper	Shapovalov, 1941

^a Type of pathogen transmission system is given as P (persistent) or N (nonpersistent).

ble 4.2). The pattern of disease incidence reflects the influence of density on insect behavior. In some cases, there are actually more infected plants in the dense stands, but a lower proportion of the stand is infected (Shapovalov et al., 1941; Heathcote, 1970, 1974; Power, 1987). This no doubt reflects the dilution of a limited number of infected colonists, resulting in a limited number of primary infections. Although absolute vector abundance increases with increasing host density, abundance per plant decreases and leads to fewer inoculations. In other cases, both the proportion and the absolute number of infected plants are lower in dense stands, again as a result of the effects on vector colonization (Hull, 1964; A'Brook, 1964, 1968; Davies, 1976; Johnstone et al., 1982).

4.3.3 Plant Quality and Fertilization

Another mechanism that may be involved in vector response to cropping system is a response to changes in host plant quality as a consequence of changes in density or diversity. Increasing overall plant density may cause stunting (Mayse, 1978) or a decrease in "lushness" (Farrell, 1976a). In some cases, the reduced attractiveness of dense stands may simply reflect a response to lower quality hosts, but this is certainly not always true. For example, Mayse (1978) corrected for plant biomass and leaf area in his comparisons of leafhopper abundance in sparse and dense plantings, and demonstrated a reduction in leafhopper abundance in dense stands that was independent of plant size.

Insect preference and performance can be strongly influenced by the quality of the host plant as a food resource. Although "quality" is a

complex concept and may incorporate many physiological and morphological characteristics of the host plant, certain characteristics have been shown to be very important for herbivorous insects. The growth and reproduction of most insects are limited by the nitrogen content of the host plant (Southwood, 1973; McNeil and Southwood, 1978; Mattson, 1980). Aphids and leafhoppers perform better on plants that are high in soluble nitrogen (Auclair, 1963; van Emden et al., 1969; Prestidge, 1982), and preference may depend on the presence or absence of individual amino acids (van Emden and Bashford, 1969, 1971; Prestidge and McNeill, 1982). Conversely, the absence of certain nutrients can lead to "restlessness" on the part of the insect and a tendency to leave the plant (Kennedy, 1976). In both natural and agricultural systems, applications of nitrogen fertilizer often lead to higher population levels of herbivorous insects (Scriber, 1984).

If vectors are attracted to and feed longer on plants of high quality, plants with higher nitrogen content because of phenology, nitrogen fertilization, or individual variability should exhibit higher levels of persistently transmitted diseases. For example, the incidence of beet yellows virus, which is persistently transmitted by aphids, is higher in sugar-beet fields receiving nitrogen fertilizer than in those without fertilizer (Blencowe and Tinsley, 1951; Heathcote, 1974). However, the transmission rates of nonpersistent diseases may tend to be higher on low nitrogen plants, because of increased restlessness and probing (Kennedy, 1976).

Changes in plant quality may also influence disease spread through effects on insect morphology. The nutritional status of the host plant can determine the proportion of winged and nonwinged morphs that are produced in aphid colonies, with more winged morphs usually produced on suboptimal hosts (Forrest, 1970; Kunkel and Mittler, 1971). Where secondary disease spread is important, changes in host plant quality that cause increased production of winged aphids could lead to more rapid spread.

4.4 The Corn Stunt System

The corn stunt spiroplasma is transmitted to maize by the corn leafhopper, *Dalbulus maidis* Delong & Wolcott (Homoptera: Cicadellidae), in a persistent fashion (Nault, 1980). The spiroplasma, which can be transmitted only by vector feeding, reproduces in the leafhopper but does not affect survivorship or fecundity (Madden et al., 1984). Yield losses from corn stunt are significant throughout much of Latin America (Nault, 1983; Urbina, 1982) and are severe in Nicaragua, where I carried out a series of experiments to explore the influence of cropping system on disease spread.

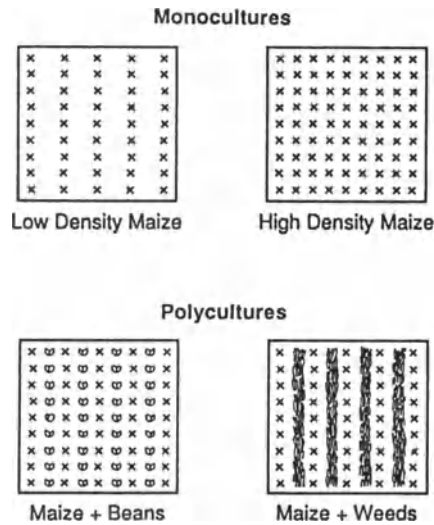


Figure 4.5. Diagram of the four experimental plant communities: low-density maize monoculture, high density maize monoculture, maize/bean polyculture, and maize/weed polyculture. $\times$ represents a maize plant, $\circ$ represents a bean plant, and w represents weeds.

Because maize/bean polycultures are a traditional cropping system in Central America, I designed an experiment to investigate the influence of intercropping with beans on the spread of corn stunt (Power, 1987). The experimental design included: (1) a control monoculture of maize planted at standard densities; (2) a second maize monoculture planted at twice the control density to examine the effects of increased plant density; (3) a maize/bean polyculture with maize planted at the standard control density; and (4) a maize/weed polyculture with maize planted at the standard density and the weeds cultivated so that they provided the same ground cover as the beans (Figure 4.5). These treatments were crossed with two levels of nitrogen application so that the potentially confounding effects of plant quality could be examined. In addition to monitoring natural leafhopper abundance and disease incidence in these treatments, I carried out studies of leafhopper movement to estimate the rate of local plant-to-plant movement and emigration rates from the different cropping systems.

Plant diversity, plant density, and plant quality all influenced leafhopper abundance and the incidence of corn stunt. Intercropping with nonhost species (beans or weeds) led to lower leafhopper abundance (Figure 4.6) and lower disease incidence (Figure 4.7), but there were no differences between the bean and weed treatments. This suggests that it is the relative densities of host and nonhost plants, rather than the number

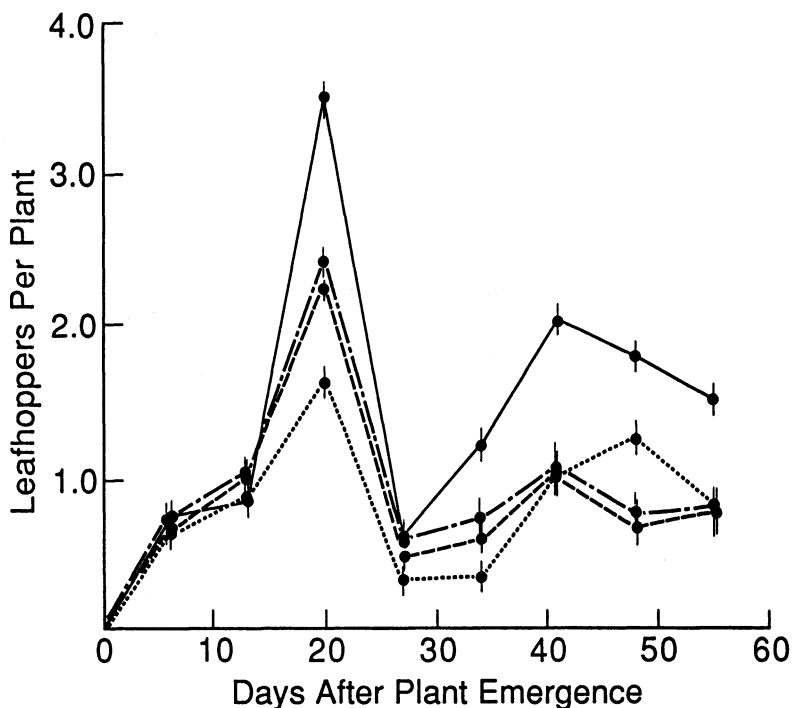


Figure 4.6. Densities of *Dalbulus maidis* per maize plant during the growing season in four experimental plant communities: low-density maize monoculture (—), high density maize monoculture (·····), maize/bean polyculture (---), maize/weed polyculture (-·-·-·). From Power (1987).

of species present, that is important for *D. maidis*. Per-plant leafhopper abundance and disease incidence were also lower in the high-density treatment (Figures 4.6 and 4.7), but this appeared to be a dilution effect: the same number of leafhoppers colonized the high and low density monocultures, but they were spread out over twice as many plants in the high density treatment. As predicted, treatments receiving lower rates of nitrogen fertilization had reduced leafhopper abundance and lower disease incidence (Figure 4.7). Because leafhopper abundance was not correlated with plant size (Power, 1985), none of these responses could have resulted from effects of plant density, diversity or fertilization on plant size.

Although differences in leafhopper abundance could account for most of the differences in pathogen incidence, *D. maidis* also had decreased plant-to-plant movement rates within polycultures and increased rates of longer distance emigration from these systems (Power, 1987). In particular, in the polyculture where beans were planted between rows of maize, rates of across-row movement were much lower than in the monocultures.

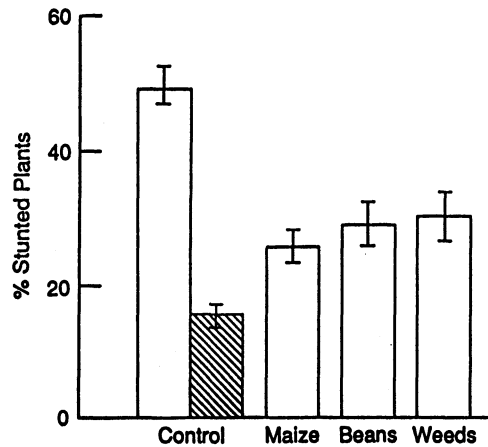


Figure 4.7. Proportion of plants exhibiting symptoms of corn stunt in five experimental plant communities: low-density maize monoculture with normal nitrogen, low-density maize monoculture with low nitrogen, high-density maize monoculture, maize/bean polyculture, maize/weed polyculture. Hatching denotes low nitrogen. From Power (1987).

That is, leafhoppers were less likely to cross a bean row than to cross bare ground. These effects on movement would contribute to lower rates of pathogen transmission independently of differences in vector abundance.

Because much of the commercial production of maize in Central America has already been converted to monoculture, and because I found that planting maize at higher densities significantly reduced the incidence of corn stunt, I further explored the influence of plant density and plant spacing on disease incidence in maize monocultures (Power, 1989). As compared to the control treatment at standard planting density, density was modified either by decreasing the distance between plants within a row or by decreasing the distance between rows. In general, leafhoppers were less abundant when the distance between plants within a row, rather than the distance between rows, was decreased. In contrast, the incidence of corn stunt tended to be lower in the treatments where the distance between rows was decreased (Figure 4.8).

This contradiction may be explained by differential effects on insect movement. Preliminary experiments suggest that insects are more likely to move from a central plant when the next host plant is closer (Power, unpublished data). Because the next plant is closer in treatments with decreased plant spacing within rows than in treatments with reduced row spacing, movement rates may be higher (Power, 1989). Such an effect on movement would mean that insects in the treatments with decreased plant spacing would encounter more plants (and presumably transmit

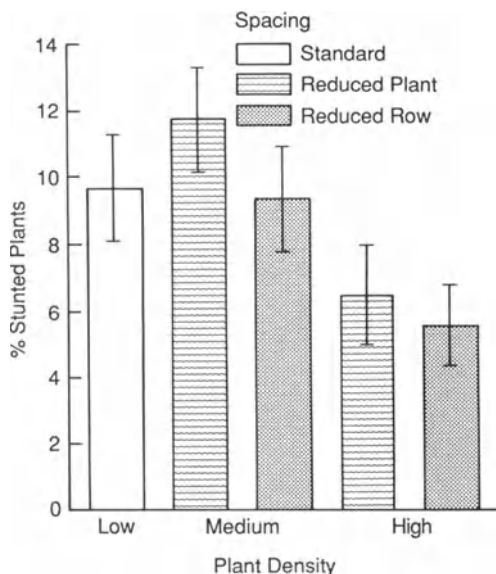


Figure 4.8. Proportion of plants exhibiting symptoms of corn stunt in low, medium, and high planting density. Hatching patterns indicate whether high densities were due to reducing spacing between plants within a row or reduced row width. From Power (1989). Copyright © 1989, Entomological Society of America. Reprinted with permission.

the pathogen to more plants), resulting in higher levels of disease despite lower vector abundance overall.

Another potential method of reducing pest damage in monocultures may be the use of varietal mixtures or multiline cultivars. With the advent of large monocultures, farmers have come to depend upon a more limited number of maize genotypes than was the case in traditional systems. This loss of genetic diversity certainly has implications for future breeding potential, but it may also influence the current dynamics of insects and pathogens attacking maize. To examine the potential for using genetic diversity as a means of cultural control in monocultures, I tested the influence of a maize varietal mixture on corn stunt incidence and vector abundance (Power, 1988).

I compared the abundance of *D. maidis* in five single-variety plantings with a mixed-variety planting consisting of equal numbers of each of the five varieties. Where leafhopper population densities were high (the Santa Rosa site), there were significantly fewer insects in the mixture than in pure stands of the component varieties (Figure 4.9). Observations suggest that this reduction is due to increased leafhopper emigration from the mixed plantings during the period of establishment in the crop (Power, 1988). At the Sebaco site with low leafhopper densities, no difference

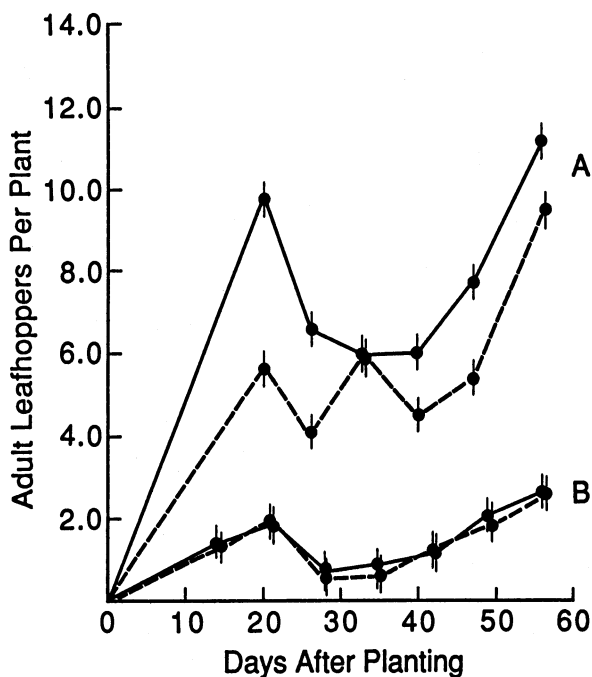


Figure 4.9. Leafhopper abundance in pure and mixed stands of maize varieties. (A) Leafhopper abundance at the Santa Rosa site. (B) Leafhopper abundance at the Sebaco site. The solid curves indicate the average number of adult *Dalbulus maidis* per plant in the five pure stands; the dashed curves indicate the mean number of *D. maidis* per plant in the mixed stand. From Power (1988).

could be discerned. Disease incidence, on the other hand, was equivalent in the mixed and single variety plantings at both sites. This lack of significant differences between mixed and pure stands may also be due to effects on movement. If leafhoppers had increased movement rates in the mixed stands, then this could result in higher rates of pathogen transmission per leafhopper, countering the effects of lower vector abundance. Thus, despite the potential for using varietal mixtures to control insect pests, such mixtures may not be useful where insect-transmitted diseases are the major cause of yield loss.

These experiments demonstrate that modifications in cropping systems could aid in reducing yield losses to corn stunt. For small farmers, the traditional use of maize/bean polycultures is clearly an effective method of controlling corn stunt. Although planting at higher densities may also reduce the incidence of corn stunt, it may not be practical if soil fertility is low and additional fertilization is not an option. On the other hand, for large systems already committed to monocultural production, increasing planting density may be a viable strategy for reducing

corn stunt. In these systems, it would be important to weigh carefully both the benefits of nitrogen fertilization in terms of grain production and the costs in terms of increased pest and disease damage. The use of varietal mixtures has some potential for both small and large producers, but the impacts on disease incidence need further evaluation.

4.5 Summary

Whereas others have stressed the importance of insect movement for the population dynamics of insect pests (Kareiva, 1985), I have focused here on the role of insect movement in the transmission of plant pathogens. I have stressed that the influence of movement may act independently of vector abundance; low vector densities could lead to high rates of pathogen transmission if movement rates are high. Thus, changes in the cropping system that affect rates of vector movement may have significant effects on disease incidence, whether or not vector abundance is affected.

Most of the important vectors of plant pathogens are homopteran insects, and these insects tend to be less abundant in plant communities of high diversity and density, due to behavioral responses to both visual and gustatory stimuli. Insect colonization, reproduction, and emigration are all involved in these responses. Although host plant quality may also change with increasing diversity or density, these factors have important effects on behavior that are independent of plant quality. Plant quality itself affects insect foraging behavior in ways that can strongly influence the transmission of insect-borne pathogens. In general, the reduced abundance of insect vectors on low quality hosts and in denser, more diverse plant communities leads to lower incidences of vectored plant diseases, but the accompanying effects on vector movement may either exaggerate or counteract these trends. It is clear that we cannot understand the epidemiology of insect-transmitted diseases in different cropping systems without first understanding the movement behavior of vector insects in response to vegetation characteristics.

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5. Diversification of Agroecosystems for Insect Pest Regulation: Experiments with Collards

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5.1 Introduction

Many studies have been conducted on agricultural systems to test the hypothesis that increased vegetational diversity fosters stability in the insect community. In a recent review of the available world literature, Andow (1983) found that in a total of 617 examples, the population densities of 66% of the monophagous herbivores studied decreased in the diversified system when compared to the corresponding monoculture. Many studies reported that predator and parasite diversity and abundance paralleled an increase in plant diversity. Others reported that the associated plant species had direct effects on the ability of herbivores to find and utilize their host plants (Table 5.1).

Numerous reviews that assemble information concerning the relationships between plant diversity and insect ecology are available (van Emden and Williams, 1974; Cromartie, 1981; Altieri and Letourneau, 1982; Altieri and Letourneau, 1984). This body of literature examines different aspects of the interaction that may be grouped as follows:

1. Studies that explain the ecological mechanisms underlying differences in the population dynamics of herbivores and associated natural enemies, under simple and complex crop habitats (Tahvanainen and Root, 1972; Root, 1973; Bach, 1980; Risch, 1980, 1981; Kareiva, 1983).

Table 5.1. Effect of increasing vegetational diversity on insect populations of crop systems

	Changes in population density ^a			Total
	Increase	No change	Decrease	
Herbivorous/monophagous				
Individuals	42	170	405	617
# spp.	15	16	92	150
Herbivorous/polyphagous				
Individuals	47	37	91	175
# spp.	21	2	13	48
Predators				
Individuals	59	48	47	154
# spp.	17	3	6	36
Parasites				
Individuals	30	7	0	37
# spp.	22	3	0	28
Total				
Individuals	178	262	543	983
# spp.	75	24	129	280

Source: After Andow, 1983.

^a Changes in population density of insects in the diversified system compared to the monoculture.

2. Papers focusing on the effects of multiple cropping patterns on insect abundance (Marcovitch, 1935; Dempster and Coaker, 1974; Litsinger and Moody, 1976; Perrin, 1977; van Emden, 1977; Altieri et al., 1978; Risch, 1979).
3. Studies that explore the consequences of maintaining various degrees of weed diversity on insect populations of crops (Pimentel, 1961; Dempster, 1969; Tahvanainen and Root, 1972; Root, 1973; Potts and Vickerman, 1974; Smith, 1976a, b; Speight and Lawton, 1976; Altieri et al., 1977; Altieri and Whitcomb, 1980; Theunissen and den Ouden, 1980; Altieri, 1981; Altieri and Todd, 1981; Altieri et al., 1981; Altieri, 1981; Horn, 1981; Gliessman and Altieri, 1982; Altieri and Gliessman, 1983).
4. Research that examines the dynamics of specific pests in perennial crop systems (orchards) with a rich floral undergrowth (Peterson, 1926; Peppers and Driggers, 1934; Bobb, 1939; O'Connor, 1950; Telenga, 1958; Chumakova, 1960; Leius, 1967; Syme, 1975; Dickler, 1978; Altieri and Schmidt, 1985).

Cruciferous crops have been used as model systems for many of these studies (Pimentel, 1981; Dempster, 1969; Tahvanainen and Root, 1972; Root, 1973; Dempster and Coaker, 1974; Smith, 1976a, b; Theunissen and den Ouden, 1980; Horn, 1981; Kareiva, 1983), and results have consistently demonstrated a decrease in herbivore abundance (particu-

larly of the specialized crucifer-feeding flea beetle, *Phyllotreta cruciferae*, the cabbage aphid, *Brevicoryne brassicae*, and a complex of Lepidoptera) when cole crops are diversified. New data emerging from two studies conducted in California that deal with these systems are presented here.

5.2 Studies on Collard/Bean Polycultures

In July 1981, an area of 3,000 m² was plowed, cultivated and divided into twenty four 5 m² plots at the University of California at Santa Cruz Agroecology Program. The distance between plots was 5 m, and these interplot areas were kept free of vegetation by frequent harrowing.

Treatments each replicated three times included:

1. Collard (var. Georgia) monoculture kept weed free by hoeing all season.
2. Collard monoculture kept weed free for only two weeks after transplanting.
3. Collard monoculture kept weed free for only four weeks after transplanting.
4. Collard monoculture weedy all season.
5. Collard/field beans (var. horticultural dwarf) polyculture kept weed-free all season.
6. Polycultures weed free for 2 weeks posttransplant.
7. Polycultures kept weed free for 4 weeks posttransplant.
8. Polycultures weedy all season.

In the mono- and polycultures, 20-day old collards were transplanted equidistantly at a density of ninety plants per plot. In the polycultures, ninety bean seeds were planted simultaneously between collards. Dominant weeds in the "weedy" plots included: *Brassica campestris*, *Raphanus* spp., *Spergula arvensis*, *Convolvulus arvensis*, and *Anagallis arvensis*.

Densities of flea beetles were estimated directly by counting the number of beetles found on ten randomly selected collard and five *B. campestris* plants in each plot on three occasions (10, 20, and 30 days after planting). At these times, the percentage of collard plants with leaves showing flea-beetle damage was recorded for each plot. Plant biomass was determined from oven dried samples of collards and weeds clipped from 1 m² quadrats at harvest time.

Table 5.2 summarizes the relevant results of this experiment. Flea-beetle (*Phyllotreta cruciferae*) densities and amount of beetle damage on collards were greater in the weed-free monoculture than in all other treatments. Interplanting beans or allowing the weeds to grow with collards considerably decreased flea beetle densities on the collards and minimized leaf damage. On the average, flea-beetle abundance was lower in the

Table 5.2. Flea-beetle (*Phyllotreta cruciferae*) densities and weed and crop biomass in various collar cropping systems in Santa Cruz, California

Cropping system*	Number of flea beetles		% collar leaves with beetle damage	Weed biomass (g/m ²)	Collard dry weight (g/m ²)
	Per 10 collard plants	Per 5 <i>Brassica</i> <i>campestris</i> plants			
Collard monocultures					
Weed free	34.0a**	ND	54.4a	0.0	213.6
4 weeks weed free	29.3b	78.1	44.6b	52.3	361.3
2 weeks weed free	29.0b	73.7	44.5b	55.2	243.0
Weedy all season	6.6c	25.0	29.9c	438.2	226.1
Collard/bean polycultures					
Weed free	2.3d	ND	34.1c	0.0	334.4
4 weeks weed free	1.6d	4.3	10.9d	25.7	324.0
2 weeks weed free	4.9c	13.1	6.7d	93.2	309.4
Weedy all season	0.6e	15.0	32.1c	234.5	115.2

Source: After Gliessman and Altieri, 1982.

* Plots were weed free or weedy all season, or were kept weed free for 4 or 2 weeks after collar transplanting, then allowed to become weedy.

** Within a column, mean values followed by the same letter are not significantly different ($p = .05$). All mean values are based on three sampling dates.

ND = no data; without weeds in the treatment, no beetles on these plants.

polyculture systems than in the monoculture systems. These herbivores exhibited very low densities on collards in the weedy polycultures, apparently due to the availability of alternate cruciferous hosts. In all "weedy" plots, flea-beetle numbers on *B. campestris* plants were greater than on collards, and this apparently diluted beetle feeding on the collards. Preferential feeding on *B. campestris* may reflect in part, differing degrees of adaptation to the foliage levels of flea-beetle-attractive glucosinolates present in each of the two plant species (Feeny, 1976). In fact, there may be considerable variation in the relative amounts of glucosinolates among cultivated and weedy crucifers (Kjaer, 1976).

5.3 Experiments With Living Mulches in Collards

In late November 1981, six of nine 10 by 10 m plots were sown with lana vetch (*Vicia dasycarpa*) at a density of 15 kg/ha at the University of California's Gill Tract Experiment Station in Albany. In three of these plots, the vetch was kept mowed, and in the other three, the vetch was allowed to grow freely. The remaining three plots were kept free of vegetation by frequent harrowings. On June 17, 1982, 8 to 12 cm tall greenhouse-grown collards (var. Georgia) were transplanted into each plot, in rows 1 m apart, with plants every 50 cm. By this time, the vetch was producing pods and reaching late maturity.

Ten collard plants within each plot were randomly selected, and sampled weekly from July 13 to August 10 by counting all alate and apterous cabbage aphids (*Brevicoryne brassicae*), including aphid mummies parasitized by *Diaeretiella rapae*, and all life stages of major insect predators. Plant height was also recorded at each sampling. Ground-living predators were studied with four pitfall traps containing water and antifreeze placed equidistantly in the center of each plot.

Figure 5.1 shows seasonal abundance patterns of alate and apterous aphids combined. These results are consistent with most authors; aphids colonized monoculture collards more readily and developed substantially higher densities thereon. In monocultures collards averaged nearly twice the height of collards present in the vetch plots. Strong competition from the vetch is doubtful because the vetch was senescent, but some kind of allelopathic effects from the vetch residues seem possible. Many crop residues contain allelopathic compounds (Steinsiek et al., 1982). Our results do not suggest that these lower aphid densities in vetch plots were due to the depressed growth of the collards. Regression analyses of collard biomass and aphid densities showed no correlation ($r = .13$ for monocultures, $r = .27$ for mowed vetch, and $r = .30$ for full-grown vetch). We believe that the attractiveness of collards to aphids decreases when collards are grown against a vetch background. Smith (1976a) found this to be the case on weedy brussels sprouts.

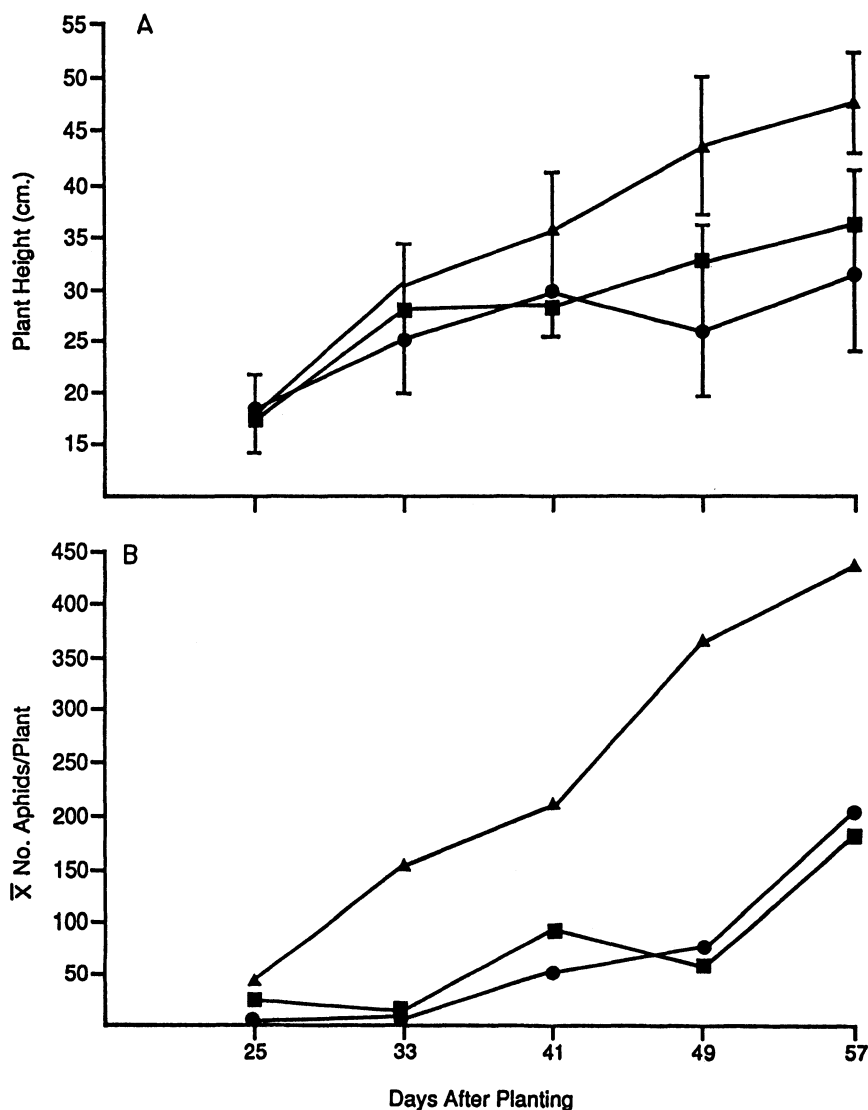


Figure 5.1. (a) Collard height growth in monoculture (▲), in systems with a living mulch of mowed vetch (■) and unmowed vetch (●). (b) Mean population densities of alate and apterous aphids (*Brevicoryne brassicae*) in collard monocultures and in collard systems with vetch living mulches.

The activity of predators could have been involved as well, but we did not find differences in predator (Chrysopidae, Syrphidae and Coccinellidae) abundance between treatments. Only ground living spiders (mainly Lycosidae, Gnaphosidae, Micryphantidae and Linyphiidae) exhibited higher densities in the vetch plots (especially in the unmowed

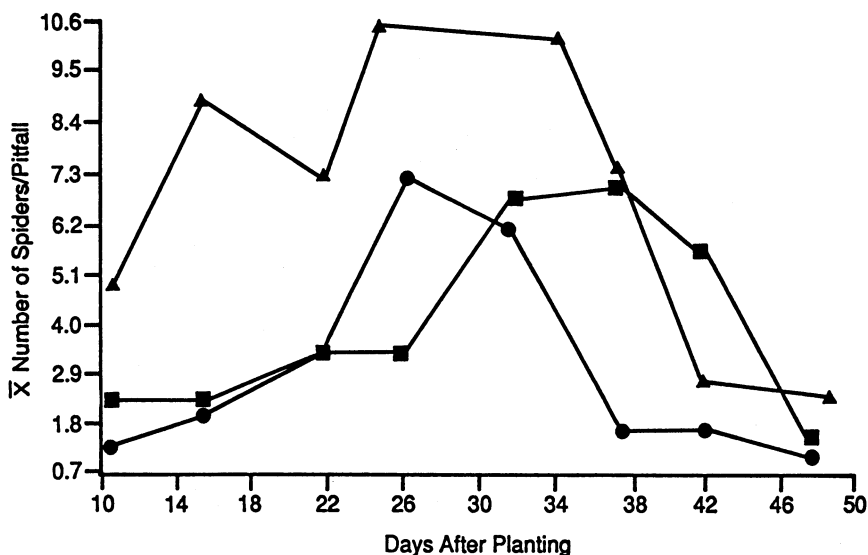


Figure 5.2. Mean number of spiders caught in pitfall traps placed in collard monocultures (▲) and in collards with a living mulch of mowed vetch (■) and unmowed vetch (●).

plots) than in the monocultures (Figure 5.2). How these increased numbers of spiders affected the aphid populations is unclear. Generally spiders are not strong aphid feeders (Turnbull, 1973). There were no apparent differences in aphid parasitization by *D. rapae* between systems.

Table 5.3 summarizes the data collected at harvest time. The between-plant variation in aphid populations stands out. Among collards in the same treatment, the coefficients of variation were consistently greater than 50%. This genuine unpredictability in the collard/aphid association makes it difficult to conform the data to the assumptions of an analysis of variance (Kareiva, 1982).

5.4 Conclusions

A vast amount of information is emerging on the effects of crop diversity on the dynamics of pests and associated natural enemies. Varied results have been obtained, and the effects seem to be pest specific and even site specific. For example, weed diversity reduced the incidence of fall armyworm, *Spodoptera frugiperda*, but not of the corn earworm, *Heliothis zea*, in Florida corn fields (Altieri and Whitcomb, 1980). Intercropping of corn and cotton exacerbated *H. virescens* damage in California and Tanzania, whereas in the Canete Valley of Peru, it aided in the control of this pest (van Emden, 1974).

Table 5.3. Effects of vetch living mulch on the densities of the cabbage aphid (*Brevicoryne brassicae*), percentage of aphid parasitization by the wasp, *Diaeretiella rapae*, and collard plant height and biomass in Albany, California

Cropping system	Aphid densities/plant			% aphid parasitization by <i>D. rapae</i>	Plant height (cm)	Collard biomass (kg, fresh weight)
	Range	Coefficient of variation	Mean + SD			
Collard monoculture	19–1945	61.5	435.5 ± 201.1	9.2a*	47.5 ± 4.8a	0.54 ± 0.16a
Collards with a mowed vetch mulch	2–1284	83.5	181.5 ± 113.6	14.5a	36.1 ± 5.1b	0.28 ± 0.10b
Collards with a full-grown vetch mulch	2–1355	91.4	204.0 ± 104.8	7.4a	31.3 ± 7.7b	0.19 ± 0.08b

* Within a column, mean values followed by the same letter are not significantly different ($p = .05$). Mean values correspond to values obtained at harvest time from 60 plants per plot.

Irrespective of location, however, all studies conducted on cruciferous crops have shown a reduction of herbivore abundance with increased vegetational diversity (Table 5.4). A few of these studies have experimentally explored the ecological mechanisms responsible for the diversity effect. These hypotheses have been discussed in detail by Root (1973), Risch (1981), and Altieri and Letourneau (1982), and by Altieri and Gliessman (1983), specifically for cole crops in California.

The results of the vetch living-mulch study reported here can be explained by the hypotheses of Smith (1976a), in that plants growing on bare soil provide ideal colonization conditions for aphids. In addition, as Dempster and Coaker (1974) found, a leguminous ground cover under the collards improves the habitat for natural enemies, which in their study translated into higher predation rates. Similar enhancements were observed when planting clover between rows of cabbages and resulted in a 34% increased depredation of eggs of the cabbage root fly, *Delia brassicae* (Ryan et al., 1980). In most situations, however, linking increased numbers of predators to increased predation of target species under field situations is a complex endeavor.

The Santa Cruz experiments revealed interactions not previously reported. Growing collards intermingled with cruciferous weeds sets up a "trap crop" system. The flea beetle is a specialized herbivore on crucifers (Feeny, 1976), and its abundance per habitat space between simple and complex collard plots was similar. However, flea-beetle densities per individual collard plant were significantly lower in the plots with crucifer weeds (mainly *B. campestris*), because these beetles preferred to feed and/or concentrate on this plant rather than on collards. The biochemical basis for this preference has been examined in studies (Altieri and Schmidt, 1985) that have found flea beetles concentrated on mustards rather than on collards, and preferentially on the flowers of mustards. When flowers were removed from experimental collard/wild mustard polycultures, flea-beetle densities increased comparable to those observed in monocultures. Other experiments showed that when offered a choice of equal numbers of collard plants treated with wild mustard extracts, mustard oil emulsions, or water, flea beetles concentrated on plants treated with wild mustard extracts and oil emulsions. Knowledge of these interactions should lead to the design of novel cropping systems, whereby wild mustards are grown in strip or border designs within collard fields. Or, margin rows in a collard field could be sprayed with wild mustard-derived attractive chemicals, thus effectively concentrating flea-beetle populations in certain sections of the field for control treatments. Other agronomic designs that minimize the competitive effect of the wild crucifers on the collards, such as keeping collards free of these weeds for 2 to 4 weeks after transplanting, and then allowing them to grow, apparently do not reduce yields, and at the same time maintain flea beetles at tolerable levels (see Table 5.2).

Table 5.4. Diversified cruciferous crop ecosystems with lower herbivore populations than in corresponding monocultures

Cropping system	Pest(s) species regulated	Factor(s) involved	References
Cabbage undersown with white and red clover	<i>Erioischia brassicae</i> <i>Brevicoryne brassicae</i> <i>Pieris rapae</i>	Interference with colonization and increase of ground beetles	Dempster and Coaker, 1974
Cabbage intercropped with tomato, tobacco, and ragweed	<i>Phyllotreta cruciferae</i>	Feeding inhibition by odors from nonhost plants	Tahvanainen and Root, 1972
Cabbage intercropped with tomato	<i>Plutella xylostella</i>	Chemical repellency or masking	Raros, 1973
Brussels sprouts with a weedy background	<i>Pieris rapae</i>	Alteration of colonization background and increase of predators	Smith, 1976a, b
Brussels sprouts intercropped with <i>Spergula arvensis</i>	<i>Brevicoryne brassicae</i> <i>Mamestra brassicae</i> <i>Evergestis forficalis</i> <i>Brevicoryne brassicae</i> <i>Plutella maculipennis</i>	Interference with colonization and predator enhancement	Dempster, 1969 Theunissen and den Ouden, 1980
Cabbage with a background <i>Crataegus</i> sp.		Provision of alternate hosts for the parasitic wasp, <i>Horogones</i> sp.	van Emden, 1965
Collards with a weedy background	<i>Myzus persicae</i>	Increased abundance of predators	Horn, 1981
Cabbage with a weedy background	<i>Brevicoryne brassicae</i>	Increase of natural enemies	Pimentel, 1961
Collards bounded by meadow vegetation	<i>Phyllotreta cruciferae</i>	Resource concentration	Root, 1973

The need to embark on large scale pilot studies of crop diversification should not continue to be neglected. The challenge is to understand the long-term limitations and potentials of this farming practice in relation to insect pest regulation, weed suppression, disease buffering, soil fertility, and crop productivity. A socioeconomic perspective should parallel the biotechnical investigations.

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6. Reduction of Damping-Off Disease in Soils from Indigenous Mexican Agroecosystems

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6.1 Introduction

Indigenous Mexican agroecosystems have been of considerable interest to the scientific community in recent years. Much attention has been focused on the archeological and agricultural significance of ancient Maya raised-field systems in the tropical lowlands of southeastern Mexico (Matheny, 1976; Turner and Harrison, 1981) and the chinampa system in the Valley of Mexico (Coe, 1964; Armillas, 1971). Most of these formerly intensively cultivated agricultural areas exist today only as relics on the landscape, often visible only from the air, and have been studied primarily from an archeological or sociological standpoint. On the other hand, the local farmers (*campesinos*) in many areas in modern-day Mexico have continued to manage several different traditional agroecosystems using time-honored farming methods. These methods balance productivity by using practices designed to sustain long-term crop production rather than maximize it on a short term basis (Gliessman et al., 1981). In addition to the more obvious effect of sustained agricultural yield, some of these systems appear to suppress or check the development of various plant diseases associated with the soil (García-E., 1980; García-E., pers. observ.).

The best known of the agricultural ecosystems still practiced in Mexico is the chinampa system, large areas of which exist in the temperate climate of the Valley of Mexico in the Xochimilco-Chalco area (Coe, 1964; Ar-

millas, 1971). The chinampas were brought to their peak of development and productivity by the Aztec empire at the time of the arrival of Cortez in A.D. 1519. Although the Aztecs developed the chinampa system extensively and used it to support a large empire and an extensive population of people, they did not originate it. The chinampas have existed in Mesoamerica for perhaps 2,000 years and are considered to be one of the most productive and intensive farming methods ever devised (Coe, 1964). The Aztecs built chinampas in swamps and shallow lakes by heaping soil and muck into ridges about 2,000 m long and 40 to 80 m wide (Armillas, 1971). The surrounding canals and ditches drain the fields and provide water for the crops. The soil is maintained by incorporating large amounts of aquatic vegetation, primarily water hyacinths (*Eichornia crassipes*) (Gliessman et al., 1981) into the soil, along with muck from canal bottoms and farm animal manures. Each plot has been described as a built-in compost heap (Coe, 1964), enabling maintenance of fertility and productivity in these soils for centuries.

In contrast to the chinampas, the popal or marceño (March planting) agroecosystem is less intensively cultivated because of its dependence on the short duration of the dry season in the tropical lowlands of Mexico (Orozco-Segovia and Gliessman, 1989). During the rainy season (June to February), large areas of the lowlands are flooded. When these flooded areas dry out, usually in March, local residents, many of them still of Chontal Indian stock, use this dry season to cultivate maize. The predominant marshland vegetation in these areas is popal (*Thalia geniculata* L.), which is cut with a machete in March and allowed to dry. Maize seeds (four to six grains) are planted in holes 10 to 15 cm deep and 90 to 100 cm apart. The drying vegetation is burned 3 to 4 days after planting for weed control purposes, but the burning does not harm the newly germinating maize seedlings. The residues of maize plants, herbaceous weeds, and organic debris brought in by flooding contribute to the formation and conservation of a highly productive organic soil, generally 30 cm or more deep (Orozco-Segovia and Gliessman, 1989).

Recent changes in both areas of Mexico threaten the continued practice of these agroecosystems. These changes include introduced modern agricultural technology, large-scale farming and cattle raising, use of pesticides and inorganic fertilizers, lowering of the water table by drainage, and use of water by large urban areas (Armillas, 1971; Gliessman et al., 1981). Because of the threat to these unique systems of agriculture, the suspected benefit of these practices in the reduction of soilborne disease problems, and the recently intensified interest in identifying and understanding the nature of disease suppressive soils (Schnieder, 1982), we have examined these two systems in relation to soilborne disease suppression. Understanding the phenomenon of suppression may provide information on potential biocontrol systems that may be exploited for modern agricultural adaptation. Consequently, we have investigated the soils

in relation to comparable soils under modern cultivation, with regard to physical and biological properties as they relate to damping-off diseases caused by *Pythium* spp. Portions of this work have been previously published (Lumsden et al., 1987).

6.2 Materials and Methods

6.2.1 Soils

Soil was collected from four sites in Mexico; two from the temperate Valley of Mexico and two from the tropical state of Tabasco: (1) soil designated chinampa-sano (CHS) was an organic, silty, clay loam from a chinampa field continuously planted to lettuce (several crops/year), maintained in the traditional manner and located near the village of San Gregorio Atlapulco, Xochimilco district; (2) Chapingo (CHA) soil was a sandy loam from an experimental plot on which various crops (e.g., broad bean and corn) were grown and maintained with modern agricultural practices (use of herbicides, fungicides, inorganic fertilizers) and located on the campus of the Colegio Postgraduados, Chapingo, Mexico; (3) popal (POP) soil was an organic, silty clay from the traditional marceño system continuously planted to corn during the dry season, and located near Cárdenas, Tabasco, Mexico; and (4) Tabasco (TAB) soil was a silty clay soil, cropped continuously to corn, using modern agricultural practices and located at the Colegio Superior de Agricultura Tropical, Cárdenas, Tabasco, Mexico. The physical and chemical properties of the four soils, listed in Table 6.1, were determined by standard procedures at the Rutgers University Soil Testing Laboratory.

Approximately 5 kg of each soil type was shipped to the Soilborne Diseases Laboratory at each sampling time. The soils were sieved (7-mm screen opening) and stored on arrival in plastic bags at room temperature before use.

6.2.2 Pathogen Populations and Disease Incidence

Populations of *Pythium aphanidermatum* (Ed.) Fitz. and *P. ultimum* Trow in the soils were assayed with differentially selective isolation media (Lumsden et al., 1975) for each batch of soil. *Rhizoctonia solani* Kuehn was enumerated with a beet-seed colonization method (Papvizas et al., 1975).

Natural disease incidence in the soils was assayed at 21°C and 32°C in temperature-controlled greenhouse cubicles (temp. range $\pm 2^\circ\text{C}$). Radish seeds (*Raphanus sativus* L. cv. 'Scarlet Globe') or cucumber seeds (*Cucumis sativus* L. cv. 'Salvador') were planted, ten per pot with six replicates, in 50 ml of soil placed on 50 ml white quartz sand in plastic pots (6 cm diameter). Healthy seedlings and those affected by pre- and

Table 6.1. Physical and chemical factors of traditional, Mexican agroecosystem soils (Chinampa and Popal) compared with modern agricultural soils (Chapingo and Tabasco)

Variable	Unit of measure	Soil*			
		Chapingo	Chinampa	Tabasco	Popal
Soil type	—	Sandy loam	Silty, clay loam	Silty clay	Silty clay
pH	[H +] ⁻¹	6.8a	5.8c	6.3b	6.4b
Water retention at -1 bar	%	5.7d	25.4b	16.1c	28.9a
Organic matter	%	3.4c	17.5b	1.9c	25.2a
Phosphorus	kg/ha	103b	202a	50c	70c
Potassium	kg/ha	319bc	656a	214c	574ab
Calcium	kg/ha	4913c	6157b	5760b	9506a
Magnesium	kg/ha	1047b	1317a	1306a	1128b
Nitrate-N	µg/g	21d	162a	38c	133b
Ammonium-N	µg/g	1.8c	3.3b	1.5c	5.4a
Cation exchange capacity	meq/ml	12.5a	38.0a	41.0a	34.0a
Soluble salts	µg/g	240c	1310a	230c	720b

* Values in each row followed by the same letter are not significantly different according to Duncan's multiple range test ($p = .05$), similar to Fisher's Least Significant Difference (LSD) test.

postemergence damping-off were counted after 1 and 2 weeks of incubation at each temperature. Diseased seeds or seedlings were removed from the soil, gently washed with running tap water, and plated on 2% water agar or media selective for *Pythium* spp. (Lumsden et al., 1975). After incubation at room temperature for 1 to 3 days, fungi growing from the infected tissues were isolated in pure culture and identified. Pathogenicity of isolates of *Pythium* spp. was determined using oat-kernel inoculum in a Beltsville sandy-loam soil as previously described (Lumsden et al., 1976). *Fusarium* spp. isolates were tested for pathogenicity in petri dishes with water agar at room temperature using a 5 mm plug of inoculum for ten cucumber seeds per dish.

Disease suppression was assayed by infesting each soil with 0, 50, 100, and 200 oospores of *P. aphanidermatum*, obtained as described previously (Ayers and Lumsden, 1975). The soils were planted with ten cucumber seeds in six replicate containers as described above and incubated at 32°C for 1 week. Disease suppression was expressed as a conducive index (C.I.) devised by Henis et al. (1978):

$$\text{C.I.} = \frac{A - x}{A}$$

in which A equals the number of healthy plants in the noninfected soil

and x equals the number of healthy plants in the infected soil. The smaller the conducive index, the greater the amount of disease suppression in the soil. Five separate batches of soils were assayed for disease suppression from January to August 1982. Disease incidence was assessed in the soils sterilized in a Gamma Cell model 220 cobalt 60 irradiator (Atomic Energy of Canada, Ltd.). The soils were exposed to 4 megarads of radiation.

6.2.3 Antagonist Populations and Microbial Activity

Microorganisms potentially antagonistic to *P. aphanidermatum* were monitored in the soils at each sampling time. Selective media for specific groups of fungi and bacteria included a medium selective for *Trichoderma* spp. (Papavizas and Lumsden, 1982), *Fusarium* spp. (Komada, 1975), *Pseudomonas cepacia* Burkholder (Burbadge et al., 1982), *Pseudomonas* spp. (fluorescent types) (King et al., 1954), and actinomycetes (El-Nakeeb and Lechevalier, 1963). Assays for populations were done for each soil batch with at least four replicate samples.

Microbial activity in the soils was determined by a dehydrogenase assay method (Skujins, 1973). The results were expressed as the μ l of hydrogen transferred and reflected substrate oxidation in the soil.

Another measure of microbial activity, the ability of the soils to inhibit germination of *P. aphanidermatum* oospores, was carried out with a modified fungi stasis assay (Adams et al., 1971). Oospores of *P. aphanidermatum*, obtained as previously described (Ayers and Lumsden, 1975), were applied to Millipore filter membranes with a diameter of 3 cm. The filters were buried vertically in 50-ml volumes of each soil previously amended with 0., 0.05, 0.10, and 0.20% asparagine (w/w, asparagine/soil). Soil was then carefully pressed against the surfaces of the filter. The soils were incubated for 16 hours at 30°C, and the filters were recovered, stained, and examined microscopically for percentage germination of oospores. This test was replicated four times for each soil and performed on two batches of soil.

Survival of oospores of *P. aphanidermatum* and *P. ultimum* was determined by burial of spores trapped in nylon mesh as previously described (Lumsden, 1981). Nylon pieces containing oospores of each *Pythium* species were recovered from each soil after 3 days and 1 and 2 weeks. Thick-walled oospores were counted, and their numbers and appearance compared to oospores in nylon mesh not buried in soil. This test was carried out on two batches of soil.

Survival of mycelia of *P. aphanidermatum* was examined also on nylon mesh (100 mm openings). *Pythium* was grown for 3 days on nylon placed aseptically on cornmeal agar. The mesh that contained intertwined mycelial strands was floated on soil extract that was prepared by mixing 200 g soil in 1000 ml distilled water, allowing the soil to settle for 5 days, at

room temperature and filtering through No.1 Whatman paper. After 1, 2, and 3 days of incubation in each soil extract, the number of mycelial strands remaining in a 400× magnification microscopic field were counted. The numbers were compared for each of the four soils tested.

Data were analyzed using the Statistical Analysis System for Analysis of Variance, Duncan's multiple range test, and correlation coefficients.

6.3 Results

6.3.1 Pathogen Populations and Disease Incidence

Pythium spp. were detected in all four soils using selective media (Table 6.2). However, *P. ultimum* and other low temperature *Pythium* spp. (*P. irregulare* and an unidentified nonoospore-forming strain) were detected only in the temperate Valley of Mexico soils. The largest populations were in the chinampa soil with generally a tenfold difference in numbers compared to those in the Chapingo soil. These species were never detected in the tropical Tabasco soils. *Pythium aphanidermatum* was consistently found at low levels (1 to 20 propagules/g soil) in both tropical soils but only in the Chapingo soil from the temperate region. An unidentified, spiny, oogonial type was associated with all four soils. Pathogenicity tests indicated that this spiny, oogonial type was not pathogenic to radish or cucumber seedlings; whereas, selected isolates of *P. aphanidermatum* and *P. ultimum* were pathogenic. *Rhizoctonia solani* was found in all soils at relatively low levels (0.8 to 6.2%) as detected by a beet seed colonization method. Differences were not detectable between comparable soils.

Assessment of damping-off of radish seedlings at 20°C and cucumber seedlings at 30°C indicated greater disease incidence in the modern, cultivated soils than in the comparable traditional systems (Table 6.2). When

Table 6.2 The populations of *Pythium aphanidermatum*, *P. ultimum* and *Rhizoctonia solani* and the incidence of damping-off of radish and cucumber seedlings

Soil	Propagules/g*		R. solani colonization**	% damping-off	
	<i>P. aphan- idermatum</i>	<i>P. ultimum</i>		Radish 20 °C	Cucumber 30 °C
Chapingo	8.1a***	254b	6.2a	56.7b	33.3a
Chinampa	0.0b	3530a	5.3a	19.2cd	14.2b
Tabasco	1.8a	0c	0.8b	75.0a	18.3b
Popal	2.9a	0c	1.0b	4.2d	2.5c

* Numbers estimated on 5 batches of soil with use of selective media for *P. aphanidermatum* and *P. ultimum*.

** Percentage colonization ($\bar{X}$ of 3 batches of soil) of beet seed added to soil, incubated 3 days, recovered, and plated on water agar.

*** Values in each column followed by the same letter are not significantly different at $p = .05$, according to Duncan's multiple range test.

damped-off seedlings were recovered from the soils, surface disinfected, and plated on water agar or selective media, *Pythium* spp. and *Fusarium* spp. were consistently recovered. *Pythium ultimum* was usually associated with plants in the Chapingo and chinampa soils incubated at 20°C, and unidentified nonsporulating fungi from the Tabasco and popal soils at this temperature. *Pythium aphanidermatum* was isolated from the Chapingo, Tabasco, and popal soils. Selected isolates of these fungi, tested for pathogenicity in the greenhouse, generally were pathogenic on cucumber seedlings. The fusaria were most frequently identified as *F. solani* (Mart.) Sacc. Only two isolates in forty produced symptoms on cucumber seedlings when grown on water agar, inoculated, and incubated at room temperature.

Further biological tests relating to disease suppression and pathogen behavior in soil emphasized *P. aphanidermatum* because: (i) *P. aphanidermatum* was present in soils from both the temperate and tropical environments, but was absent from the chinampa soil; (ii) it was present in relatively low levels in the Chapingo, Tabasco, and popal soils in the form of oospores; and (iii) it was consistently pathogenic to cucumber seedlings. *P. ultimum* was not chosen because of the relatively high populations in the temperate soils and its total absence in the tropical soils.

6.3.2 Disease Suppression

Suppression of damping-off, measured by the total number of healthy cucumber seedlings remaining in each of the four soils after one week of incubation, was assessed in five separate batches of soil collected and shipped to Maryland over an 8 month period. In each case, the number of healthy plants in the chinampa and popal soils was significantly greater than in the Chapingo and Tabasco soils without added inoculum (Table 6.3). In addition, when oospores of *P. aphanidermatum* were added at 50, 100, and 200 per ml of soil, the number of healthy plants remained relatively high in the chinampa soil at all three levels of inoculum, but decreased in the Chapingo soil with as few as 50 oospores per ml added inoculum (Table 6.3). The same differences occurred in the popal soil compared to the Tabasco soil, except when 200 oospores/ml were added. In this case, the level of oospores apparently overcame the suppressive effect of the soil.

In order to express the disease-suppressing ability of the soils, the conducive index of Henis et al. (1978) was applied to the data. This index expresses the ability of the soil to support disease based on the number of healthy plants with and without added inoculum. The smaller the index, the less likely the soil is to support disease. No significant differences in the conducive index were found when five batches of soils were averaged. Because the Chapingo and Tabasco soils supported large amounts of disease in two of the five batches, even without added in-

Table 6.3. Cucumber plant stand and conducive index in soils

Variable	Unit of measure	Soil*			
		Chapingo	Chinampa	Tabasco	Popal
Healthy plants	%				
0 inoculum		43c	62b	60b	83a
50 oospores/ml		9c	46b	23c	68a
100 oospores/ml		20b	55a	32b	65a
200 oospores/ml		16b	56a	18b	28b
Conductive index**					
50 oospores/ml		0.75a	.11c	.56a	.27b
100 oospores/ml		0.46a	.06b	.43a	.19ab
200 oospores/ml		0.56b	.00a	.69a	.69a

* Values in each row followed by the same letter are not significantly different according to Duncan's multiple range test ($p = .05$), similar to Fisher's LSD test.

** Conducive index (CI) = number of healthy plants with no added inoculum (H) minus number of healthy plants with added inoculum (X) divided by H; $(H - X/H)$.

oculum, the variability between batches apparently invalidated the comparison. For this reason three of the five batches were selected for the analysis (Table 6.3). In this case, the chinampa soil had a significantly smaller conducive index at all three levels of inoculum. With the Tabasco/popul comparison, only the lowest level of inoculum showed significant differences. The mean of the three batches for the four soils with 0, 50, and 100 oospores per ml added is depicted graphically in Figure 6.1.

6.3.3 Biological Activity in Soils

To test the effect of the soil's biological activity on disease suppression, the soils were sterilized by gamma radiation. In all soils, the disease incidence was greatly increased by the sterilization (Figure 6.2). In fact, with the addition of 200 oospores/ml to the sterilized soil, 100% of the cucumber seedlings were killed in the Chapingo, Tabasco, and popal soils. Only in the chinampa soil did about 20% of the plants escape infection.

Additionally, the biological activity of the soils was measured by a dehydrogenase assay method, which estimated the transferral of hydrogen electrons during substrate oxidation. In three replicated experiments, the biological activity was two to three times greater in the traditionally cultivated soils than in those under modern agricultural management (Table 6.4, Figure 6.3).

Biological activity was also determined by estimating the effect on germination of oospores of *P. aphanidermatum* when the soils were amended with several levels of the amino acid asparagine (Figure 6.4). Significant suppression of germination was evident in both the chinampa and the popal soils, compared to the Chapingo and Tabasco soils when the same amount of exogenous nutrient was supplied to each soil (Table 6.4).

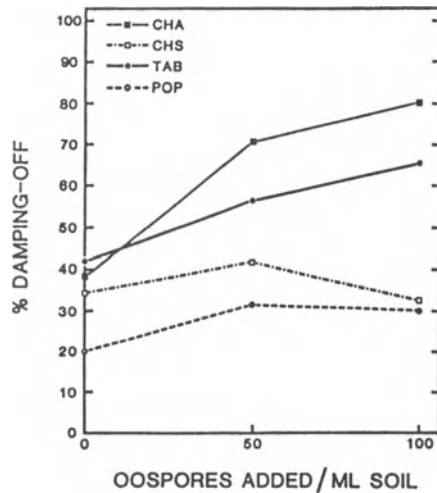


Figure 6.1. Incidence of damping-off of cucumber seedlings in Mexican soils (CHA = soil from Chapingo, Mex.; CHS = chinampa soil from Xochimilco, Mex.; TAB = Tabasco soil from Cárdenas, Tabasco, Mex.; and POP = popal soil from Cárdenas, Tabasco, Mex.) infested with 0, 50, and 100 oospores of *P. aphanidermatum* per g soil. Soils were incubated for one week at 30 °C in the greenhouse.

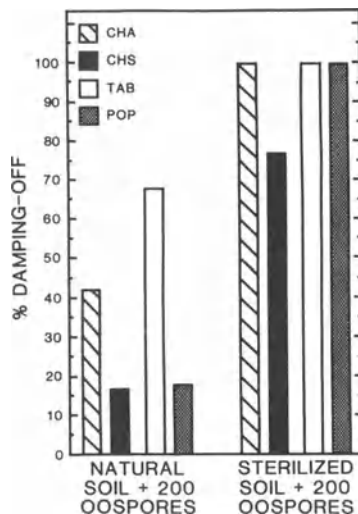


Figure 6.2. Effect of sterilization with gamma irradiation (4 megarads) on incidence of cucumber damping-off in soils from traditional agroecosystems (CHS = chinampa, POP = popal), compared to soils from modern agroecosystems (CHA = Chapingo, TAB = Tabasco) with the addition of 200 oospores of *P. aphanidermatum* per g soil. Soils were incubated for 1 week at 30 °C after planting.

Table 6.4. Biological activities and populations of selected microorganisms in soils

Variable	Unit of measure	Soil*			
		Chapingo	Chinampa	Tabasco	Popal
Dehydrogenase		35b	125a	36b	120a
Oospore germination with 0.1% asparagine	$\mu\text{l H}_2$ transferred/g				
Oospore survival	%	35b	15c	41a	12c
Exp. 1		8b	17b	75a	76a
Exp. 2		24b	4c	54a	17b
Mycelial survival		12.4a	9.0b	9.6bc	8.5bc
Population of potential antagonists	$\bar{X}$ hyphae/field				
<i>Trichoderma</i> spp.	Colony-forming units (c.f.u.)	3786b	1607b	3793b	22964a
<i>Fusarium</i> spp.		7984b	22520a	5560bc	3320c
<i>Pseudomonas cepacia</i>		857b	2843b	56214b	155514a
<i>Pseudomonas</i> spp. (fluorescent)		8053b	176316a	28368b	182632a
Actinomycetes		$6.3 \times 10^6\text{a}$	$5.9 \times 10^6\text{a}$	$4.8 \times 10^6\text{a}$	$5.1 \times 10^6\text{a}$

* Values in each row followed by the same letter are not significantly different according to Duncan's multiple range test ($p = .05$), similar to Fisher's LSD test.

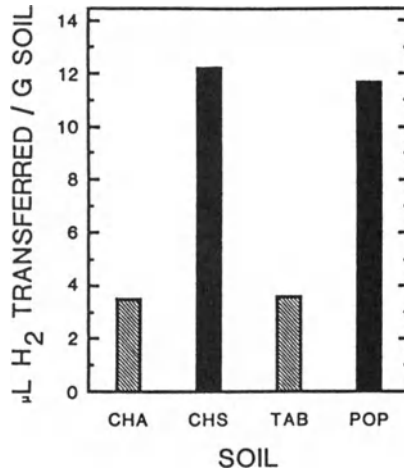


Figure 6.3. Total microbial activity measured by dehydrogenase activity (μL hydrogen transferred/g soil) in Mexican soils from traditional agroecosystems (CHS = chinampa, POP = popal) compared to modern agricultural system soils (CHA = Chapingo, TAB = Tabasco).

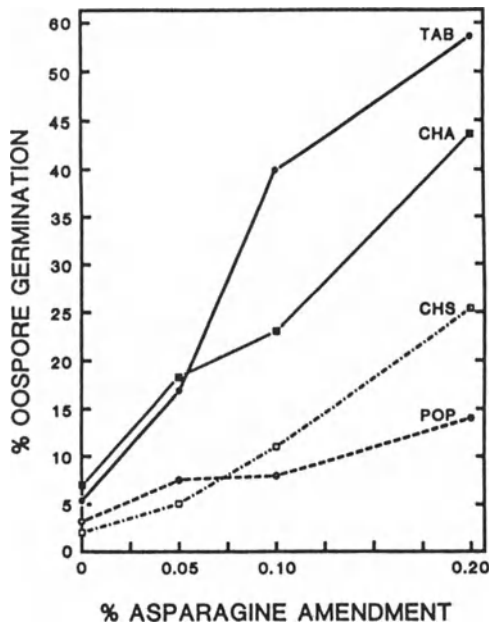


Figure 6.4. Percent germination of oospores of *Pythium aphanidermatum* in Mexican soils from traditional agroecosystems (CHS = chinampa, POP = popal) compared to soils from modern agricultural systems (CHA = Chapingo, TAB = Tabasco) in the presence of 0, 0.5, 0.10, and 0.20% asparagine.

Survival of mycelia and oospores buried in the soils was not consistently measured (Table 6.4), but oospores were invaded by various microorganisms in the soil, especially in the temperate soils. When the oospores or their remains were recovered from the soils, removed from the nylon mesh support, and plated on water agar, a large number of fungi, actinomycetes, and bacteria were isolated in pure culture and identified. The frequency of occurrence of these microorganisms was difficult to assess because of the different rate at which the oospores deteriorated, the different degrees of deterioration, and the degree of difficulty in isolating the microorganisms in pure culture. Certain types of microorganisms were predominant however, and were thought to have originated from within decomposing oospores. The main types identified were *Fusarium* spp., mainly *F. solani*, *Humicola fuscoatra* Traaen, *Penicillium* spp., *Verticillium chlamydosporium* Goddard, and *Streptomyces* spp. These and numerous other species, including *Farrowia longicollaea* (Krzem. & Badura) D. Hawksw., *Gliocladium catenulatum* Gilm. & Abbott, *Paecilomyces lilacinus* (Thom.) Samson, all isolated from oospores, and *Pseudomonas* spp. and *Trichoderma* spp. isolated from the soils, were tested for their ability to decrease disease caused by *Pythium* spp. in Sassafras sandy loam in the greenhouse. Results of this study have been presented (Lumsden et al., 1982, 1987) and demonstrated that several of the fungal isolates have disease-suppressive capabilities.

Populations of five potential antagonists, for which selective media were available, were monitored during the study period (Figure 6.5). When the temperate soils were compared, significantly greater numbers of colony-forming units were detected in the chinampa soil with *Fusarium* spp. and the fluorescent pseudomonads (Table 6.4) than in the Chapingo soil. When the tropical soils were compared, higher numbers of *Trichoderma* spp., *P. cepacia*, and fluorescent pseudomonads were found in the popal soil than in the Tabasco soil. Notable differences existed between the temperate and tropical suppressive soils. *Fusarium* spp. were more numerous in the temperate soils than the tropical, and *Trichoderma* spp. and *P. cepacia* were more numerous in both the tropical and the temperate suppressive (traditional) soils than in the soils under modern agricultural practice.

6.3.4 Physical Properties

Between comparable pairs of soils the following differences were significant with the respective physical parameters (Table 6.1): Organic matter, potassium, nitrate, ammonium, and calcium contents, as well as soluble salts, and water retention were higher in the suppressive chinampa and popal soils than in their respective modern-system soils. Magnesium was higher in the chinampa than the Chapingo, but did not differ between the popal and Tabasco. The pH was higher in the Chapingo than the

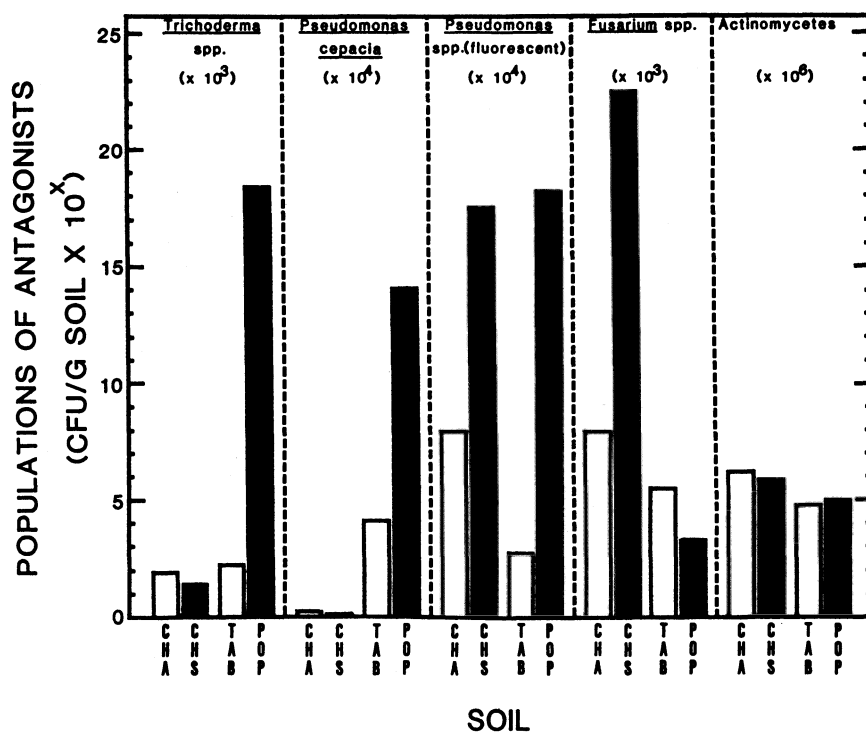


Figure 6.5. Populations (colony-forming units/g) of potentially antagonistic *Trichoderma* spp., *Pseudomonas cepacia*, *Pseudomonas* spp. (fluorescent), *Fusarium* spp. and actinomycetes in Mexican soils from traditional agroecosystems (CHS = Chinampa, POP = popal) compared with modern agricultural systems (CHA = Chapingo, TAB = Tabasco).

chinampa, but did not differ between the popal and Tabasco. The pH of the Chapingo and chinampa soils changed from 7.4 and 6.4, respectively, at the beginning of the study, to 6.8 and 5.8, respectively, at the end. Other values for physical factors remained relatively constant during the course of the study.

6.3.5 Interaction of Parameters

Correlation coefficients were determined for each of the physical and biological variables in relation to the number of healthy plants obtained in the temperate soils (chinampa and Chapingo) to which 100 oospores of *P. aphanidermatum*/ml were added and in the tropical soils (popal and Tabasco) to which 50 oospores/ml were added (Table 6.5). Highly

Table 6.5. Correlation coefficients for selected variables for comparison of numbers of healthy cucumber plants in pairs of contrasting Mexican soils

Variable	Correlation coefficients*	
	Temperate soils ^a	Tropical soils ^b
	Healthy plants with 100 oospores/ml	Healthy plants with 50 oospores/ml
Soil properties		
pH	-.92**	.77
Organic matter	.91**	.84*
Moisture at -1 bar	.91**	.62*
Phosphorus	.93**	.83*
Potassium	.90**	.86*
Calcium	.88*	.85*
Magnesium	.89**	-.90**
Nitrate-N	.90**	.06
Ammonium-N	.86**	.55
Biological activity ^c		
<i>Fusarium</i> spp.	.83**	-.65*
<i>Pseudomonas cepacia</i>	.82**	.68*
<i>Pseudomonas</i> spp. (fluor.)	.59**	.63*
<i>Trichoderma</i> spp.	-.89**	.68*
Dehydrogenase	.84**	.80*
Oospore germination	-.90**	-.45

^a Traditional chinampa agroecosystem soil and modern system soil from Chapingo, both from the temperate Valley of Mexico.

^b Traditional popal agroecosystem soil and modern system soil from the tropical areas near Cárdenas, Tabasco, Mexico.

^c Biological activity includes colony-forming units of microorganisms, the dehydrogenase activity as a measure of total microbial activity, and germination of oospores of *Pythium aphanidermatum* in the soils.

* $p = .05$.

** $p = .01$.

significant positive correlations (greater than 85% at $p = .01$) occurred with the temperate soils in relation to organic matter, soil moisture, phosphorus, potassium, magnesium, nitrate, and ammonium, and significant positive correlations occurred in relation to calcium (at $p = .05$). A highly significant negative correlation existed between the number of healthy plants and the pH. *Fusarium* spp., *P. cepacia*, and fluorescent pseudomonads were highly positively correlated with healthy plants, as was dehydrogenase activity. Germination of oospores and *Trichoderma* spp. populations were highly negatively correlated with healthy plants.

The number of healthy plants in the tropical soils (popal and Tabasco) were positively correlated ($p = .05$) with organic matter, soil moisture, phosphorus, potassium, calcium, nitrate, and ammonium, but negatively correlated with magnesium. Positive correlations were calculated for *P.*

cepacia, fluorescent pseudomonads, and *Trichoderma* spp., but negative correlations for *Fusarium* spp. and oospore germination with regard to incidence of healthy plants.

6.4 Discussion

Damping-off disease of cucumbers and radishes caused by *P. aphanidermatum* was consistently less in the traditional chinampa and popal soils in this study than in the comparable modern Chapingo and Tabasco soils. *P. aphanidermatum* did not occur naturally in chinampa soil, although it did occur in the comparable, temperate-climate Chapingo soil. It occurred in low levels in both tropical soils.

Significant levels of disease suppression were exhibited in both the chinampa and popal soils in response to added inoculum of *P. aphanidermatum*. There are other reports of soils naturally suppressive to *Fusarium* spp., *R. solani*, *Phytophthora cinnamomi*, and *Gaeumannomyces graminis* (Smith and Snyder, 1972; Baker and Cook, 1974; Broadbent and Baker, 1975; Alabouvette et al., 1979; Papavizas and Lumsden, 1980; Scher and Baker, 1980; Chet and Baker, 1981; Cook, 1981; Schneider, R. W., 1982). These examples fall into three general groups of natural disease biocontrol as described by Cook (1981): (1) the pathogen will not establish; (2) it establishes but produces no disease; and (3) it produces disease but then declines.

With *P. aphanidermatum*, the first two possibilities exist in this study. In the chinampa soil, the pathogen did not exist, possibly because of its failure to become established. Once it was introduced, it produced significantly less disease at comparable inoculum levels than in the Chapingo soil, where it was established at low levels. *Pythium ultimum* was also apparently suppressed in the chinampa soil. In this case, however, the pathogen was established, in fact at ten-fold higher levels than in the Chapingo soil. It was apparently less able to cause damping-off in the chinampa soil than in the Chapingo soil even at 20°C and at the high inoculum levels (Table 6.2)

Natural disease suppression can be attributed to physical factors (Baker and Cook, 1974; Schneider, 1982) and to the soil microbiota (Baker and Cook, 1974; Papavizas and Lumsden, 1980; Schnieder, 1982). Antagonistic effects of the microbiota toward pathogens include destruction of pathogen propagules, reduction of germination of propagules, inhibition of growth and lysis of mycelia in soil, and competition for substrates and nutrients (Papavizas and Lumsden, 1980).

Physical factors and biological factors both appear responsible for the decreased incidence of damping-off by *Pythium* spp. with natural inoculum and introduced inoculum of *P. aphanidermatum* in the chinampa

and popal soils. The enhanced suppression was reflected in the significantly smaller conducive indices at all levels of inoculum added to the chinampa soil compared to the Chapingo soil, and the low level of inoculum added to the popal soil compared to the Tabasco soil (Table 6.3). The suppressive ability was partially destroyed in the chinampa soil and totally destroyed in the popal soil by gamma radiation (Figure 6.2). Destruction of suppression by sterilization of soil is indicative of a biological mechanism for the suppression (Schneider, 1982).

In support of a biological cause of suppression is the enhanced microbial activity in the chinampa and popal soils, shown by the increased levels in the dehydrogenase activity in these soils (Figure 6.3). In addition, the activity of *P. aphanidermatum* in these two soils was significantly repressed, as shown by the much-reduced ability of oospores of the fungus to germinate at increasing levels of added nutrient (Figure 6.4). Both of these sets of supporting data indicate a general type of biological suppression, perhaps reflecting the total microbial competition and accompanying elevated levels of fungistasis (Papavizas and Lumsden, 1980). Increased levels of fungistasis and the resulting decreased spore germination have been implicated in enhanced *Fusarium*-wilt suppression in a naturally suppressive soil (Smith and Snyder, 1972) and in soil induced to be suppressive by addition of chicken manure (Homma et al., 1979).

Specific factors responsible for disease suppression are difficult to pinpoint but probably have greater significance in explaining disease suppression than the more general factors. Mycoparasitism of pathogen propagules can be at least partially responsible for pathogen suppression (Papavizas and Lumsden, 1980). Although we were unable to show consistent differential effects of mycoparasites on survival of *P. aphanidermatum* in the comparative soils, presumed parasites were isolated from deteriorated oospores, obtained in pure culture, and some of them used to successfully reduce disease in greenhouse studies.

Some of the genera represented among these antagonists were monitored during this study using selective media. In this way we were able to follow population levels of *Fusarium* spp., *Trichoderma* spp., *Pseudomonas* spp. (fluorescent types), *P. cepacia*, and actinomycetes (Figure 6.5). In the temperate chinampa soil, *Fusarium* spp. and fluorescent pseudomonads were consistently present in higher numbers than in the Chapingo soil. In the tropical popal soil, *Trichoderma* spp. (primarily *T. harzianum* Rifai), *P. cepacia*, and fluorescent pseudomonads were consistently more numerous than in the Tabasco soil.

The *Fusarium* spp., primarily *F. solani*, were apparently mostly saprophytic, with some isolates capable of reducing *P. aphanidermatum* damping-off in greenhouse studies (Lumsden et al., 1982) and in a single field test (Lumsden, unpublished results). Saprophytic *F. oxysporum* and *F. solani* were thought to play a key role in the suppressive properties of soils in which melons were grown repeatedly in France (Alabouvette et

al., 1979). The suppressive effect was transferable but was not active against *Pythium* spp., *Phytophthora* spp., or *R. solani*. Protection was thought to be achieved by prior occupancy of the ecological niche required by the pathogen.

Trichoderma spp., most numerous in the popal soil, also showed antagonistic capabilities in greenhouse pot studies. Approximately ten-fold differences in numbers of propagules of *Trichoderma* spp. were present in the popal soil compared with the Tabasco soils. This antagonist likely could play a major role in disease reduction. *Trichoderma* is perhaps the most commonly used fungus for purposes of biocontrol (Papavizas, 1985), and it has been associated with naturally suppressive soil (Chet and Baker, 1981).

Pseudomonas cepacia was consistently associated in high numbers ($\bar{X}$ 1.5×10^5 /g soil) with the popal soil, and also expressed disease control capabilities as seed inoculant in greenhouse pot studies (Lumsden et al., 1982). This bacterium has previously been demonstrated to have biocontrol ability toward *Fusarium* damping-off of onion (Kawamoto, 1976).

The only organisms monitored in this study that were associated with both the temperate and tropical suppressive soils were the fluorescent pseudomonads. This is a species-group of bacteria containing *P. fluorescens*, *P. putida* and others. Disease suppressive soils have been described suggesting that these bacteria may contribute to the mechanism of suppression (Kloepper et al., 1980; Scher and Baker, 1982; Weller and Cook, 1983). Strains of the bacteria have been successfully applied for biocontrol of disease caused by *Fusarium* spp. (Scher and Baker, 1980), *G. graminis* (Weller and Cook, 1983), and *P. ultimum* (Howell and Stipanovic, 1980). These bacteria, because they were associated with soils from dissimilar climates and have been associated with disease suppression in several instances, may be important in their contribution to disease suppression in these traditional agricultural soils. Perhaps the biological factors associated with disease suppression in these soils constitute a complex of interactions that need exploration for adequate identification of the responsible components.

The physical factors associated with disease suppression include soil pH, organic matter, and nutrient content. The pH of the chinampa soil may contribute at least partially to the suppression of *P. aphanidermatum* added to this soil. This fungus does not germinate well in soils below pH 6.0 (Adams, 1971; Lumsden et al., 1976). Although at the beginning of this study, the pH of the chinampa soil was higher (pH 6.4) the values decreased over the course of the study to a low of pH 5.6. This low pH could account for at least a portion of the disease suppression, the lack of total destruction of suppressive ability by gamma irradiation, and for a portion of the suppression of germination. The pH of agricultural soils has previously accounted for the failure of *P. aphanidermatum* to germinate and proliferate in low pH soils (Lumsden et al., 1976). In the

latter instance, and also with the chinampa soil, the pH of the soil did not affect the behavior of *P. ultimum* in the soil, or apparently, disease suppression. Soil reaction has been implicated in other cases of disease suppression ability (Lui and Baker, 1980; Scher and Baker, 1980). The soil reaction was likely not the sole factor responsible for disease suppression in the case of the chinampa soil, but in combination with the soil, biological activity may have actually prevented establishment of this ubiquitous pathogen in the chinampa soil. The pH played no significant role in the popal soil suppression, because no differences in pH were noted between it and the Tabasco soil.

Organic matter in the chinampa and popal soils was significantly higher in the more suppressive soils (Table 6.1). Organic matter has been implicated in instances of disease increase and disease decrease (Papavizas and Lewis, 1981; Lumsden et al., 1983). There are several examples of decrease in disease being associated with increased organic matter content of the suppressive soils (Broadbent and Baker, 1975; Lumsden et al., 1976; Homma et al., 1979; Chet and Baker, 1981). In fact, organic soils in Australia that are suppressive to *P. cinnamomi* on avocado (Broadbent and Baker, 1975) were similar to the chinampa soil in that copious quantities of organic matter in the form of crop debris, green manures, and animal manure were added over a period of years. It was proposed that the high organic matter content in the Australian soils improved soil structure and moisture-holding capacity, and provided a complex microflora antagonistic to plant pathogens (Broadbent and Baker, 1975). Mineral nutrient content was higher in the organic, traditional soils than in the comparable modern soils. This was consistently the case with calcium, potassium, magnesium, and nitrogen. These minerals would be expected to be high with the addition of large amounts of organic matter to the soil. Calcium, especially, has been implicated in the disease suppressiveness of Australian avocado soils (Broadbent and Baker, 1975). High calcium in this case was suggested as affecting soil structure and host nutrition.

Apparently, in the chinampa and popal agroecosystems, a dynamic biological equilibrium exists, in which intense management, especially the addition of copious quantities of organic matter, maintains levels of organic nutrients and calcium, potassium, and other mineral nutrients. These stimulate the biological activity in the soil. The elevated biological activity, especially of known antagonists, such as *Trichoderma* spp., *Pseudomonas* spp., and *Fusarium* spp., can suppress the activity of *P. aphanidermatum*, other *Pythium* spp., and perhaps other soilborne plant pathogens.

Two types of disease suppression appear to operate in these soils. "Short-term" suppression operates on the basis of increased microbial activity, which reduces the pathogen's ability to germinate in soil and cause disease. This type of suppression may exist in both the chinampa

and popal soils. A second type of suppression, "long-term", operates over a relatively long period of time and affects the survival of the pathogen. With *P. aphanidermatum*, perhaps a combination of factors, including increased biological activity of the soil, mycoparasitic activity, the slightly lower pH in the case of the chinampa soil, and the periodic flooding in the popal system (García-E., 1980), interacted to decrease the incidence and disease-causing ability of this pathogen.

These two agroecosystems illustrate the value of intense management of agricultural production. Although management of organic matter in agricultural soils is sometimes difficult, the use of organic materials, such as soil amendments, can be beneficial (Papavizas and Lewis, 1981; Lumsden, et al., 1983), especially if sources of organic matter are readily available.

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7. The Role of Allelopathy in Agroecosystems: Studies from Tropical Taiwan

Chang-Hung Chou

7.1 Introduction

Allelopathy, a botanical term originated by Molisch (1937), means literally the reciprocal suffering of two organisms. The term has since appeared in literature to refer to plant/plant biochemical interactions that have detrimental effects. Autointoxication has been regarded as a type of allelopathy where an organism releases a toxic chemical that suppresses its own growth. Allelopathy has now been recognized as an important ecological factor in plant interactions. Allelopathic compounds are released into the environment by means of volatilization, leaching, decomposition of residues, and root exudation (Börner, 1960; Muller, 1966; Chou and Chen, 1976; Chou and Lin, 1976; Young, 1984). These processes are also affected by environmental factors, and it is very difficult to single them out in the environmental complex (Koeppel et al., 1971; Muller, 1979; Koeppel et al., 1976; Harborne, 1977; Chou, 1983; Rice, 1984; Einhellig, 1987; Waller, 1987). In the last decade, a tremendous growth of publications on allelopathy has occurred (Börner, 1971; Whitaker and Feeny, 1971; Chou and Muller, 1972; Gliessman and Muller, 1978; Rice, 1984; Lovett, 1986; Putnam and Tang, 1986; Anaya et al., 1987; Chou, 1987; Grodzinsky, 1987; Waller, 1987). Recently, allelopathy has been concerned in a broader scope of research involving sustainable agriculture that is known to be organic, alternative, regenerate, biodynamic, intensive, low input, or resource conserving. In many parts of the

world, allelopathy was used in agricultural practice, such as weed control, intercropping systems, nutrient-cycling mechanisms, and low, external-input agriculture (Chou, 1986; Elliott and Cheng, 1987; Fisher, 1987; Gajić and Nicočević, 1973; Gliessman, 1983, 1986, 1987; Grodzinsky, 1987; Rizvi and Rizvi, 1987). Since 1972, Chou and his co-workers have conducted such research in a humid zone of Taiwan and accumulated substantial information concerning allelopathic interactions in various habitats. The findings of studies of allelopathy are of great significance in clarifying the role of allelopathy in the agroecosystem.

7.2 Allelopathy and Yield Reduction in Monoculture

7.2.1 Low Yield of Rice in the Second Crop Season

Rice (*Oryza sativa*), the most important crop in Taiwan, is planted twice a year in a continuous monoculture system. Since 1901, it has been noted that the yield of the second crop is generally lower by about 1000 kg/ha (approximately 25%) than the first crop (Wu and Antonovics, 1979). This reduction of rice productivity has been particularly pronounced in areas of poor water drainage. Between the first crop season (from March to July) and the second (from August to December), the fallowing period is only 3 weeks, as compared with a 10-week period elsewhere. During the fallowing period, the farmers always leave rice stubble in the field after harvesting, incorporating the residues into the soil for decomposition. It was found that during decomposition, a great quantity of phytotoxins were produced, resulting in the suppression of rice growth and subsequent grain yields (Tables 7.1 and 7.2) (Chou and Lin, 1976; Chou et al., 1977; Chou and Chiou, 1979; Chou et al., 1981). Aqueous extracts of paddy soil collected in Nankang were bioassayed and found to be phytotoxic (Chou and Lin, 1976; Chou et al., 1977). In pot experiments, a rice straw and soil mixture (100 g : 3 kg) was saturated with distilled water and allowed to decompose for 1, 2, and 4 weeks under greenhouse conditions. Soil alone was treated in the same manner as a control. At the end of each decomposition time, five rice seedlings (3 weeks old) were transplanted into the soil. After 1 month, control rice seedlings were normal and usually over 66 cm tall, whereas the seedlings grew poorly (about 36 cm tall) in the straw and soil mixture. The roots of retarded plants were dark brown, and the root cells were abnormal and enlarged (Chou and Lin, 1976; Chou et al., 1977). Further experimental results showed that phytotoxicity increased with increased additions of straw, and the toxicity of aqueous extracts of decomposing rice residues was still persistent after 16 weeks of decomposition. The rice straw and soil mixture with different intervals of decomposition was extracted with ethanol, the extracts were subsequently purified, and the phytotoxins

Table 7.1. Phytotoxic phenolics produced during decomposition of rice residues

Compound	Soil treatment					
	NH ₄ -N			NO ₃ -N		
	Content, ppm		Ratio	Content, ppm		Ratio
	S ^a	SR		S	SR	
Ferulic acid	4	12	0.33*	2	14	0.14*
<i>trans-p</i> -coumaric acid	14	21	0.66*	11	20	0.55*
Syringic acid	6	11	0.54*	8	11	0.72*
Vanillic acid	11	13	0.85	10	16	0.63*
<i>p</i> -Hydroxybenzoic acid	10	11	0.91	8	11	0.73*
<i>cis-p</i> -coumaric acid	1	1	1.00	3	7	0.43*

Source: Part of data from Chou and Chiou, 1979.

^a The pot was filled with 10 g soil (S) or with soil mixed with 100 g chopped rice (SR), and applied with nitrogen fertilizers.

* Statistical significance at 1% level.

present in the extract were identified by chromatography. The compounds identified were *p*-coumaric, *p*-hydroxybenzoic, syringic, vanillic, *o*-hydroxyphenylacetic, and ferulic acids (Chou and Lin, 1976), as well as acetic, propionic, and butyric acids (Wu et al., 1976b). *O*-hydroxyphenylacetic acid, earlier reported to be a phytotoxin (Chou, 1983), was par-

Table 7.2. Yield components of rice plants in pot soils

Yield component (per hill)	Soil treatment					
	NH ₄ -N			N ₃ -N		
	Content, ppm		Decrease %	Content, ppm		Decrease %
	S ^a	SR		S	SR	
Panicle number	38.75	32.25	17	26.25	19.50	26*
Total panicle weight (g)	64.33	58.24	10	52.25	42.26	20
Ripening rate (%)	90.90	89.13	1	97.65	92.70	5
Testing weight (g/100 seeds)	27.00	27.16	0.5	28.01	26.01	7
Grain weight (g)	61.85	55.24	11	50.26	40.14	21*
Yield (g/m ²)	1546.30	1380.90	11	1256.40	1003.57	20*

Source: Part of data from Chou and Chiou, 1979.

^a The pot was filled 10 kg soil alone (S) and the soil was mixed with 100 g chopped rice straw (SR), and applied with nitrogen fertilizers.

* Statistical significance at 5% level.

ticulatory toxic to rice growth at a concentration of $1.64 \times 10^{-4}M$. We found that the concentration of *o*-hydroxyphenylacetic acid reached about $10^{-2}M$ in the soil containing decomposing rice residues (Chou and Lin, 1976).

7.2.2 The Yield Reduction of Sugarcane

Poor germination and growth of ratoon cane have been found to be the two major problems in the farms of the Taiwan Sugarcane Corporation (TSC). The yield of monoculture sugarcane has declined in many sugar cane fields. The causes of this yield reduction have been investigated, but no single factor causing the reduction can be found. Wang et al. (1967) demonstrated by field and laboratory experiments that phytotoxic effects are one of the important factors involved. Five phenolic acids (*p*-hydroxybenzoic, ferulic, *p*-coumaric, syringic, and vanillic) and formic, acetic, oxalic, malonic, tartaric, and malic acids were identified in the decomposing sugarcane leaves in water-logged soil. A $3 \times 10^{-4}M$ solution of these phenolic acids in water culture inhibited the growth of young sugarcane roots. The aliphatic acids were also found to inhibit the growth of ratoon sugarcane at $10^{-3}M$ (Wang et al., 1967). Furthermore, Wu et al. (1976) found that the population of *Fusarium oxysporum* was greater in the rhizosphere soil of poor ratoon cane roots than in that of good ratoon roots. They found that fusaric acid, a secondary metabolite of the organism, was toxic to the growth of young sugarcane plants *in vitro* (Wu et al., 1976). Nevertheless, Wang et al. (1984) conducted an experiment with a flooding treatment on the low-yield sugar cane field and found that the population of *F. oxysporum* decreased tremendously, compared with fields that were not flooded. They also found that the amount of fusaric acid was significantly lower in the soil that was subjected to flooding. These findings clearly indicated that the flooding treatment may improve the rhizosphere of sugarcane soil, allowing the population of *Fusarium* to reach a homeostasis with other soil microorganisms; thus the amount of phytotoxins produced decreased.

7.2.3 Autointoxication of *Asparagus officinalis* L.

Asparagus officinalis is a perennial ratoon crop widely planted in Taiwan. A significant reduction of yield and quality of asparagus often occurs in old plantation soil. The wilting of asparagus plants has been found to be the result of monoculture. Young (1984) indicated that there was about 40% loss of asparagus seedlings from the plantation. Young further showed that the root exudates of asparagus retarded the seedling growth of asparagus cultivars, namely Mary Washington, California 309, and California 711 (Young, 1986). Exudate collected by use of circular trapping with a XAD-4 resin significantly retarded radicle and shoot growth of asparagus seedlings (Young, 1984). Six phytotoxic phenolics, namely

3,4-dihydroxybenzoic, 3,4-dimethoxybenzoic, 2,5-dihydroxybenzoic, 3,4-dimethoxyacetophenone, 3,4-dihydroxyphenylacetic, and β -(*m*-hydroxyphenyl)propionic acids were found in the extracts and exudates of asparagus plant parts. The amount of phytotoxins was significantly higher in the stem than in the root, and was highly correlated to phytotoxicity (Young, 1986). It is concluded that the reduction of asparagus productivity in old asparagus fields is primarily because of phytotoxins released from the plant parts and those produced from the decomposition of residues remaining in the soil.

7.2.4 The Yield Reduction of Pangola Grass

In Taiwan, pangola grass (*Digitaria decumbens*) has been a highly productive pasture and a dominant grassland species; however, its productivity declines several years after planting. Chou and his associates found that the pangola grass produced phytotoxins that suppressed its own growth (Liang et al., 1983). Therefore, a crop rotation system of pangola grass/watermelon/pangola grass was established. The watermelon was planted in the drought winter season and pangola grass was planted in the spring season, following the harvest of watermelon. The yield of pangola grass after watermelon was significantly increased by about 40%, compared to that without the rotation. It is assumed that the increase of grass production after rotation of watermelon could be a result of the disappearance of phytotoxins produced by pangola grass, and further experimentation needs to be conducted in order to clarify the mechanism of autotoxic effect.

7.3 Allelopathic Mechanisms of Some Aggressive Grasses

7.3.1 Allelopathic Dominance of Native and Pasture Grasses

Miscanthus floridulus, widely distributed in Taiwan, is a dominant native grass and often occurs in poor soil on hillsides and/or channels. A field experiment conducted at a Nankang hillside showed that the botanical composition in *Miscanthus* stands is about 65% *M. floridulus*, 17% *Lactuca indica*, and less than 4% in another ten weed species (Chou and Chung, 1974). A successional trend in botanical composition is caused by the aggressive nature of *Miscanthus floridulus*. For example, the dominance of *Miscanthus* was reestablished three years after it was removed by weeding, with the suppression of associated species found in *Miscanthus* stands (Chou, 1983). Furthermore, aqueous extracts of *Miscanthus* leaves caused a significant reduction of radicle growth of tested species (Figure 7.1). The extracts of soils collected from the *Miscanthus* rhizosphere, between stands, under the canopy of *Miscanthus*, and in open ground control area adjacent to the *Miscanthus* stands revealed phyto-

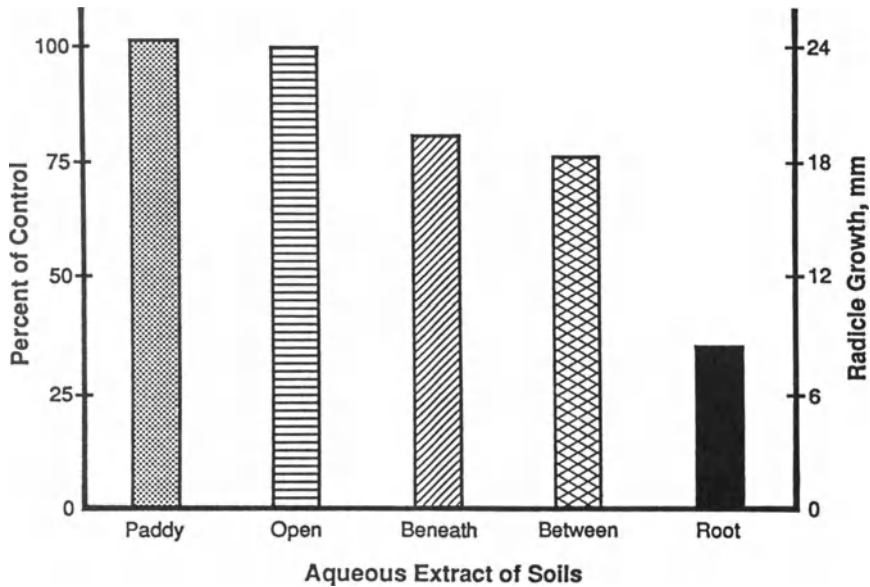


Figure 7.1. Comparison of effects of aqueous extracts of soil collected from paddy field (Paddy), open ground area (Open), under the canopy of *Miscanthus* (Beneath), between the stands of *Miscanthus* (Between), and the rhizosphere of *Miscanthus* (Root) on the radicle growth of lettuce seedlings. The distilled water was used as control solution for assay.

toxicity to some extent. The extract of root soil of *Miscanthus* exhibited the highest inhibition of the tested plants (Chou, 1983).

The aqueous leaf extracts of twelve forage grasses were evaluated for their phytotoxicity to several tested species. Among them, *Acroceras macrum*, *Cynodon dactylon*, *Chloris gayana*, *Digitaria decumbens*, *Eragrostis curvula*, *Panicum repens*, and *P. maximum* always caused significant inhibition of radicle growth of test plants. *Digitaria decumbens* had the highest phytotoxicity. All extracts had an osmotic concentration of 10 milliosmols, at which the osmotic inhibition is zero (Chou and Young, 1974; Chou and Young, 1975).

7.3.2 Evaluation of an Allelopathic Grass For Weed Control

An increased amount of allelopathy research on grassland species has been conducted in many parts of the world during recent decades (Muller, 1971; Chou and Muller, 1972; Newman, 1978; Rice, 1984). Most of the studies have been concerned with the interpretation of allelopathic phenomena in the field. Only a few studies have employed the allelopathic effect as a practical means of directly controlling weeds (Putnam and

Duke, 1974; Liang et al., 1983). In Taiwan, many grasses have been introduced into pasture but only a few varieties can be established as forage pasture. As already mentioned, among twelve species studied (Chou and Young, 1975), pangola (*Digitaria decumbens*) exhibited the highest toxic effect on test species. Under sufficient nitrogen fertilizer application, pangola grass forms a pure stand where almost no other weeds can grow. We also found that different varieties of pangola had different growth performance and competitive ability. Liang et al. (1983) selected eight varieties of pangola for field trials and laboratory assays. These showed that the invasion ability of cultivars A65, A255, and A254 were highest in Hsinhwa, Hengchun, and Hwalien stations, respectively; whereas cultivars A79 and A80 were inferior in all stations. Cultivars A84, A254, and A255 possessed significant phytotoxicity, which was due primarily to nine phytotoxic phenolics identified (Liang et al., 1983). The interference of grasses in the field is very complicated, and allelopathy alone cannot account for the complicated phenomena. Other forms of plant interference, especially nutrient and water competition, must also be examined.

7.4 Allelopathy in Forest Ecosystems

7.4.1 Allelopathic Nature of Some Bamboo Species

On many hillsides in the mountainous districts in Taiwan, there are vast areas of bamboo plantations. Beneath the canopy of bamboos, the ground is relatively bare of understory species. This phenomenon was thought to be an allelopathic effect; however, the pattern varies with species. Thus, Chou and his associates conducted experiments to evaluate the potential of allelopathic effect in fourteen common bamboo species in Taiwan (Chou and Hou, 1981). The bioassay results of aqueous extracts of leaves of 14 bamboo species showed that *Sinocalamus latiflorus* possessed the highest phytotoxicity for lettuce, rye grass, and rice plants; in addition, *Bambusa oldhami*, *B. pachinensis*, *B. ventricosa*, *Phyllostachys edulis*, and *P. makinoi* also showed significant phytotoxicity. Aqueous extracts obtained from the associated bamboo soils also exhibited some inhibition, which in most extracts was correlated with that of leaf extracts (Chou and Kuo, 1986). Particularly in the Chitou area, *Cryptomeria japonica* (conifer) and *Phyllostachys edulis* (bamboo) grow adjacent to one another. However, the *P. edulis* often encroaches on the *C. japonica*, resulting in the gradual decline of productivity and ultimately the death of the conifers (Chou and Yang, 1982). A comparison of the floristic composition of the two vegetations showed that the understory species respond differently to either light intensity or to phytotoxic leachates. The total number and dry weight of seedlings/m² meter were much higher in the conifer com-

munity than in the bamboo forest, although the light intensity, soil moisture, and soil nutrient content were significantly higher in the bamboo habitat. Chou and Yang (1982) found that the litter of *Phyllostachys edulis* possesses phytotoxic phenolics that suppress the growth of its understory. Further results indicated that the aqueous extracts and leachates of bamboo leaves were more phytotoxic than those of conifer leaves. The continuous release of water-soluble phytotoxins from *P. edulis* and the accumulation of these in the soil may result in suppression of understory growth or the elimination of neighboring plants.

7.4.2 Allelopathic Effect of *Leucaena leucocephala*

Leucaena leucocephala trees have been widely planted in Taiwan because of their high economic value for producing nutritious forage, firewood, and timber. Generally, after a few years of growth, the floors of these plantations are relatively bare of all understory plants except *Leucaena* seedlings. This pattern of weed exclusion beneath *Leucaena* trees is particularly pronounced in areas having a drought season.

A *Leucaena leucocephala* plantation was studied at the Kaoshu village of Pintung county, situated in the southern part of Taiwan. After 3 to 4 years of growth, there was an almost total lack of understory, except for *Leucaena* seedlings during the winter season. The absence of weeds is because of a heavy accumulation of *Leucaena* plant residues, such as leaf litter, branches, etc. Chou and Kuo (1986) found that the biomass of ground cover beneath *Leucaena* plantations was relatively low, compared to its adjacent grassland control area (9.3 g/m² on the *Leucaena* floor and 330 g/m² in the grassland area). There was about 80% bare ground under *Leucaena*. The amount of litter accumulated under *Leucaena* was remarkably high (1027 g/m²), accentuated by a dry winter season and heavy wind.

Chou and Kuo (1986) conducted a series of experiments in the field, greenhouse, and laboratory. Field data showed that the phenomenon was not primarily because of physical competition, light, soil moisture, pH, or nutrients. Instead, aqueous extracts of fresh leaves of *Leucaena*, seeds, litter, and soil showed significant phytotoxic effects on many test species, including rice, lettuce, *Acacia confusa*, *Alnus formosana*, *Casuarina glauca*, *Liquidambar formosana*, and *Mimosa pudica*. However, the extracts were not toxic to *Leucaena* seedlings. Decomposing leaves of *Leucaena* also suppressed the growth of the aforementioned plants grown in pots but did not inhibit growth of *Leucaena* plants. Ten phytotoxins were identified using paper and thin-layer chromatography, uv-visible spectrophotometry, and high performance liquid chromatography. They included mimosine, quercetin, and gallic, protocatechuic, *p*-hydroxybenzoic, *p*-hydroxyphenylacetic, vanillic, ferulic, caffeic, and *p*-coumaric acids. The mature leaves of *Leucaena* contain about 5% (dry weight) of mimosine,

the amount varying with the variety. Seed germination and radicle growth of lettuce, rice, and rye grass were significantly inhibited by aqueous mimosine solutions at a concentration of 20 ppm, whereas that of the forest species mentioned was suppressed by mimosine solutions at 50 ppm or above. However, the growth of *Miscanthus floridulus* and *Pinus taiwanensis* was not suppressed by a mimosine solution at 200 ppm. Seedlings of *Ageratum conyzoides* died in mimosine solution at 50 ppm within 7 days and wilted at 300 ppm within 3 days. It is concluded that the exclusion of understory plants is because of the allelopathic effect of compounds produced by *Leucaena*. The allelopathic pattern was most clearly shown in the area with a heavy accumulation of *Leucaena* leaf litter during a year with drought and heavy winds.

7.5 Allelopathy in Pasture/Forest Intercropping System

7.5.1 Kikuyu Grass and Chinese Fir

Taiwan is an island, with two thirds of the land occupied by mountains, and its forests are extremely important for water conservation. The limited amount of agricultural land for crops and pasture forces farming activities to move upward to hillsides and higher elevations. A forest/pasture intercropping system has been thought to be a possible way to increase livestock production. Recently, we have conducted several experiments in the forest area of Hoshe Experimental Station of National Taiwan University located at an elevation of about 1200 m. An area of about 1 hectare was deforested; part was cleaned by removing the leaf litter of the coniferous tree (*Cunninghamia lanceolata*), and part was left unchanged to serve as control. The cleaned and unchanged plots were planted with kikuyu grass (*Pennisetum clandestinum*) or left open. The experiment was designed to determine the reciprocal interaction of fir litter and kikuyu grass, and to evaluate the allelopathic potential of the two plants on weed growth under natural conditions. Results (Table 7.3) indicated that the biomass of kikuyu grass in the cleaned plot was significantly higher than that in the control plot. In addition, the number of weeds that grew in the plot planted with kikuyu grass was lower than that in the control plot, indicating that the kikuyu grass may compete with and suppress weeds. The seedlings of fir that regenerated in the deforested area grew well and seemed not to be affected by the neighboring, newly planted kikuyu grass. However, the growth of kikuyu grass was inhibited by the fir litter left on the unchanged plot in the first 3 months after deforestation. Furthermore, bioassay of aqueous extracts showed that the fir litter extract exhibited higher phytotoxicity than the kikuyu grass. Nevertheless, 4 months after deforestation, the kikuyu grass

Table 7.3. Effects of field treatments on weed and kikuyu grass

Plant	Relative coverage, %		Biomass, kg/8 m ²		Number of seedlings	
	Left (Control)	Removed	Left (Control)	Removed	Left (Control)	Removed
Kikuyu grass	42	70*	5.00	5.50*	ND ^a	ND
Weed	58	30*	0.61	0.35*	25	17*

Source: Reorganized from Chou et al., 1987.

^a ND = no data; it is not possible to measure the number of seedlings for the stoloniferous type of kikuyu grass.

* Statistical significance at 5% level.

growth in the field was luxuriant, indicating that the phytotoxicity of fir litter disappeared (Chou et al., 1987).

7.5.2 Beneficial and Phytotoxic Effect of Cover on Orchard Plants

Recently, Chou and one of his students (Chen, 1985) conducted experiments at Meifeng Highland Experimental Station of National Taiwan University, located at Nantou County, to evaluate the competitive and allelopathic nature of nine cover plants (*Bromus catharticus*, *Dactylis glomerata*, *Eragrostis curvula*, *Lolium multiflorum*, *L. perenne*, *Paspalum notatum*, *P. dilatatum*, *Pennisetum clandestinum*, and *Trifolium repens*). Of them, *L. multiflorum*, *B. catharticus*, and *D. glomerata* exhibited the highest yields. *L. multiflorum*, *T. repens*, and *P. clandestinum* established a ground cover most rapidly, but the yield of the latter two species was comparatively lower. The phytotoxicity of leaf extracts of the nine plants was also evaluated, and the results showed that *T. repens* and *L. perenne* exhibited highest phytotoxic potential. However, root exudates of the nine plants stimulated the growth of *Pyrus lindleyi* seedlings under fertilizer dressing, and *D. glomerata* and *L. multiflorum* showed a remarkable stimulatory effect. With respect to soil conservation, covers of *P. notatum*, *T. repens*, *L. multiflorum*, *P. clandestinum*, and *O. glomerata* performed best. In addition, Wu et al. (1975) evaluated the effect of three cover crops (*Centrocema* sp., *Indigofera* sp., and *Paspalum notatum*) on growth of some vegetable crops and orchard plants. They found that *Centrocema* and *Indigofera* exhibited the highest phytotoxic effect, and leachate of *Centrocema* inhibited the growth of banana.

7.5.3 Allelopathic Effect of *Vitex negundo* on Pasture Grass

Vitex negundo is a dominant component of coastal vegetation and widely distributed in the southern parts of Taiwan. Chou and Yao (1983) found

that the biomass and density of its associated understories are relatively lower than in adjacent pasture. Field results showed that the natural leachate of *V. negundo* significantly retarded the growth of *Digitaria decumbens* but stimulated the growth of *Andropogon nodosus* when compared to the rainfall control. The growth of *D. decumbens*, grown in pots under greenhouse conditions, was significantly retarded by watering with a 1% aqueous extract of *V. negundo*, but the growth of *Andropogon nodosus* and *Mimosa pudica* was stimulated. The aqueous extract was phytotoxic to lettuce and rye grass seeds. The aqueous effluents obtained from a polyamide column chromatograph were also bioassayed. Some fractions inhibited radicle growth of lettuce and rice seedlings, whereas other fractions had a stimulatory effect. The responsible substances were isolated and identified. These included phenolic acids, *p*-hydroxybenzoic, ferulic, *p*-coumaric, vanillic, and syringic acids, and ten flavonoids, of which one was 3'-hydroxyvitexin (Chou and Yao, 1983).

7.6 Allelopathy Regulated By Environmental Factors

7.6.1 Allelopathy and Water-Logged and Oxygen-Deficient Conditions

Patrick and Mikkelsen (1971) indicated that the level of oxygen reached almost zero when it was measured at 25 cm below the soil surface in a rice paddy field. In many areas of Tsingshui (the central part of Taiwan), Chiutung and Yuanlin (the southern part), and Tungshan (the east coast), the paddy fields have poor water drainage or have a high water table, leading to oxygen deficiency. This is even more pronounced in the second crop season when the monsoon comes. In addition, the farmers in Taiwan have always submerged rice straw into soil and allowed it to decompose. During the decomposition of rice residues in soil, a significant amount of phytotoxic substances, such as short-chain aliphatic acids and phenolic acids, were produced. The accumulation of organic acids could result in the decrease of redox potential in paddy fields. Chou and his co-workers found that the soil Eh ranged from -100 to 200 mV during the first crop season in the Nankang paddy field. At the farm of the National Chungshing University of Taichung, the Eh was remarkably low, ranging from -500 to 100 mv during the second crop season. In pot experiments, we found that the soil Eh was below -300 mV in the treatment of rice straw mixed with soil, and was above 100 mV in the treatment of soil alone. Thus, the reduction of soil Eh was apparently related to the decomposition of rice residues in soil. The reduced soil Eh had the greatest effects at the tiller stage (30 to 45 days after transplanting) and at the panicle stage (80 to 90 days after transplanting) (Chou and Chiou, 1979). During this period, the growth of rice roots was retarded, the root cells swelled,

and many adventitious roots developed. Wu et al. (1976) postulated that the swelling of root cells could be an adaptive mechanism for obtaining more oxygen.

7.6.2 Allelopathy and Microbial Activity

Microorganisms are involved in the decomposition of toxic plant residues (Chou and Patrick, 1976; Patrick, 1955; Patrick, 1971; Patrick and Koch, 1963). Wu et al. (1976) found that the denitrifying bacteria *Pseudomonas putida* became dominant in the rhizosphere of the rice paddy, with populations positively correlated to both phytotoxin production when rice residues were submerged in soil, and to the poor water drainage. They pointed out that in soils of the well-drained area of Tsaotune, the number of *P. putida* was $701 \times 10^5/\text{g}$ dry soil, whereas in the poorly drained areas of Lotung, Taan, and Taichung, the number of *P. putida* was highest in the most poorly drained soil, indicating that the organism might use the rice residues as a carbon source. Wu et al. (1976) further indicated that the phytotoxic phenolics did not come from the metabolites of this microorganism but were released from the decomposing rice residues. Chou and Chiou (1979) pointed out that ammonium sulfate mixed with rice residues enhanced phytotoxicity, suggesting that the addition of nitrogen fertilizer might favor the growth of decomposing microorganisms, and thus expedite the decomposition rate of rice residues in soil. Wu et al. (1976) also indicated that the application of ammonium-sulfate fertilizer to paddy soil was beneficial to the growth of *P. putida*, but might also expedite the formation of H_2S , which is toxic to rice growth. Furthermore, Rice et al. (1981) indicated that five phytotoxic phenolics produced by decomposing rice straw and sterile extracts of decomposing rice straw in soil were inhibitory to the growth of three strains of *Rhizobium* (Table 7.4). The effects were additive and in several instances synergistic. The compounds also reduced nodule numbers and hemoglobin content in two bean (*Phaseolus vulgaris*) varieties. Extracts of decomposing rice straw in soil also significantly reduced nitrogen fixation in Bush Black-Seeded beans. Rice and Lin (1980) also reported that these five phytotoxins were inhibitory to the growth of *Anabaena cylindrica*, a nitrogen-fixing cyanobacteria.

Similarly, the cause of yield decline of sugarcane in Taiwan has been investigated by Wang and his associates (1984) and Wu et al. (1976). They found that the reduction is partly because of the phytotoxic effect of decomposing cane residues in soil, as well as the microbial activity of *Fusarium oxysporum*, which produces a phytotoxin, fusaric acid. They found that the *F. oxysporum* population was much greater in the rhizosphere of ratoon sugarcane soil than in the soil without planting. At 10 ppm of fusaric acid mixed in Murashige and Skoog's medium, leaves of sugarcane wilted and became chlorotic (Wu et al., 1976).

Table 7.4. Effects of [10^{-3} M] phenolics on the growth of 3 strains of *Rhizobium* bacteria^a

Compound	Mean radius of inhibition zone in <i>Rhizobium</i> strain, mm		
	R 10314	R 10703	R WSM
<i>p</i> -Coumaric acid	3.2	1.2*	3.0
Ferulic acid	2.5	0.2	1.2
<i>p</i> -Hydroxybenzoic acid	4.2	0.5	0.8
<i>o</i> -Hydroxyphenylacetic acid	1.2	1.0	1.2
Vanillic acid	1.5	2.0	0.9
Mixture of previous five	2.2*	1.8	0.5
<i>p</i> -Coumaric and vanillic acids	3.0*	2.2*	0.2
<i>p</i> -Hydroxybenzoic and <i>o</i> - hydroxyphenylacetic acids	1.5*	1.8*	1.0*
Ferulic acid and vanillic acid	3.5*	1.8*	0.5

Source: Data reorganized from Rice et al., 1981.

^a Control had no inhibition.

* Statistical significance at 5% level.

7.6.3 Phytotoxins and Nitrogen Availability

Chou et al. (1977) concluded that more rice stubble left in the paddy soil would lead to more phytotoxic phenolics and less leachable nitrogen, suggesting an interaction of phytotoxins with available nitrogen in soil. They also found that the amount of leachable $\text{NH}_4\text{-N}$ was about ten times as great as that of $\text{NO}_3\text{-N}$ (Chou et al., 1977). Chou and his co-workers (1982) used ^{15}N -isotope tracer techniques to study the distribution of nitrogen in soil or soil/rice residue mixtures under different temperature regimes and sequences. In the absence of straw, most of the fertilizer N remained in the mineral form. Straw enhanced N immobilization only moderately. The gradual decrease in the proportion of fertilizer N in the mineral form was accompanied by a steady increase of fertilizer N in the amino acid fraction of the organic N. Little accumulation of fertilizer N was found in the amino sugar or the insoluble humic fraction (Chou et al., 1982). Although the experimental results did not show a distinct trend in relation to temperature variations, the temperature range of 25 to 30 °C tended to favor N transformation activities.

7.6.4 Decomposing Rice Residues and Leachable Soil Cations

During the decomposition of rice residues in soil, the amount of available minerals might be affected and consequently alter plant growth. Chou and Chiou (1979) studied the effect of rice straw incorporated into soil on the dynamics of some cations in pots. The results revealed that the concentrations of the cations, K, Cu, and Mn, were higher in the first crop season, whereas those of Na, Ca, Mg, and Zn were higher in the

second crop season in Nankang paddy soil, regardless of nitrogen fertilizer application. Most of our findings agree with those of Patrick and Mikkelsen (1971). In flooded soil, the concentrations of reducible iron and manganese were relatively low. When the pot soil was mixed with rice straw and allowed to decompose, the amount of K was significantly higher than that in soil alone, but the concentrations of Cu, Fe, Mn, and Zn were, on the average, significantly lower in the soil in terms of the soils and straw ratio. It is interesting to note that in several areas in Taiwan with poor water drainage, such as Changhwa, Taitung, and Pingtung, Zn deficiency is particularly pronounced during the second crop season.

7.6.5 Cations, Soil Phytotoxicity, and Nutrient Additions

Chou and Chiou (1979) reported that the form in which nitrogen fertilizer was applied would alter yields of rice. Ammonium-sulfate fertilizer produced higher yields than nitrate-nitrogen fertilizer. Apparently, ammonium-sulfate fertilizer may overcome the phytotoxic effect of decomposing rice residues in soil. This finding agreed with that of Chandrasekaran and Yoshida (1973), who concluded that ammonium sulfate effectively eliminated the injury caused by phytotoxins. We also found that the root system of rice plants was healthy and well developed under the ammonium-sulfate dressing, compared to those under the nitrate-fertilizer dressing. In addition, Wu and her co-workers (1976) conducted field experiments in the poorly draining paddy soil of Lotung by applying ammonium sulfate, lime, and green manure to compare the phytotoxic effect of rice residues decomposing in soil. The results indicated that the paddy soil supplied with lime exhibited significantly higher yield than that with other treatments (Wu et al., 1976). They concluded that the increase of rice yield was simply due to a detoxification of phytotoxins, with calcium binding and converting them into nontoxic substances. It is concluded that some nutrients may play a chelating role in lessening soil phytotoxicity, leading to a better yield of crops.

7.6.6 Natural Detoxification Mechanism of Phytotoxins

Wang et al. (1978) found that protocatechuic acid, one of the phytotoxins related to *trans-p*-coumaric acid, and other phytotoxic phenolics can be polymerized with humic acid by using clay minerals as heterogeneous catalysts. In fact, humic acid can polymerize many kinds of substances, such as amino acids, flavonoids, terpenoids, aliphatic acids, and other nitrogen-containing compounds, thus keeping the soil in a fertile state. However, it is also possible that the polymerization of phytotoxic phenolics fixed in humic substances can be reversed under certain environmental conditions, with subsequent release of free phenolic compounds that exert a phytotoxic effect on nearby susceptible plants. If this is the case, the natural device of organomineral complexing of humic acid could

actually be a pool for the detoxification of toxic substances produced by plants (Wang et al., 1971; Wang et al., 1978; Wang et al., 1983).

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8. Nutrient Mobility in a Shifting Cultivation System, Belize, Central America

J.D.H. Lambert, D. Brubacher, and J.T. Arnason

8.1 Introduction

In recent years, the pressure on shifting cultivators to reduce the fallow periods has been increasing because of the need to produce more food for an ever growing-population. Earlier studies have reported that as much as a 15 to 20 year fallow period was required to return a two-year agricultural site to its original fertility. Data on biomass changes show rapid increases in early stages of succession (Ewel, 1971; Buschbacher and Uhl, 1987), during which time the wood tissues are important in the immobilization of cations, phosphorus (P) and nitrogen (N) (Bartholomew et al., 1953; Snedaker and Gamble, 1969; Singh et al., 1985). Brubacher et al. (1989) have shown that levels of nitrogen (N), phosphorus (P) and potassium (K) allocated to leaves peaked in year-old fallows, with little further increase in 2- and 3-year-old sites. Potassium (K) accumulated rapidly in stem material, with little increase after the first year of fallow growth, whereas N and P accumulation continued at steady rates for another 2 years of fallow development. The role of weeds in nutrient accumulation during the initial stages of secondary succession has been reported by Toky and Ramakrishnan (1983) and Lambert and Arnason (1986). The more recent studies listed above have suggested that immobilized nutrients in plant tissues can reach levels similar to the surrounding, undisturbed forest within 10 years.

Because conventional researchers have generally considered shifting cultivation (slash and burn) to be a destructive system with little merit,

they have stressed its negative qualities. Where the pressures of land use dictate increasingly shorter fallow periods, yields decline, and the reestablishment of forest species is inhibited. Prolonged use of tropical forest sites results in the increasing dominance of grass species. Such a life form, with its extensive root system that is not destroyed by short-lived but intensive fires, easily excludes other plant species. Frequent removal and/or burning of woody shoots can lead to a depletion of starch reserves in the roots and subsequent inhibition of successional species recolonization after abandonment (Miyanishi and Kellman, 1986).

A challenge to agricultural scientists is to find ways to help the shifting cultivators who are caught between a shortening fallow and lack of capital to adopt alternatives. In this situation, the key is to identify the minimal length of fallow that allows for maximum nutrient immobilization and reuse for cropping.

In this chapter, data are summarized from several years' work on traditional Maya farming systems in the Indian Church region of Belize. Nutrient dynamics are documented in a 45-year-old seasonally dry hardwood forest that was cleared and cropped for 3 years. Subsequent accumulation in a three-year fallow is documented for the area.

8.2 Nutrient Dynamics of High Bush Fallow

Vegetation in the area of Indian Church is classified as seasonably dry tropical forest (Beard, 1955). Locally known as High Bush, such forest is an extremely diverse association, with species such as *Guazuma ulmifolia*, *Stemmadenia donnell-smithii*, and *Spondias mombin* occurring most frequently. In the undisturbed High Bush we found an average of thirty-nine woody species per hectare (trees, shrubs, and woody vines).

After cutting and burning, only seven species survived, based on observations of sprouting from stumps (Figure 8.1). During the cropping period (milpa) approximately 50% of the species were herbaceous. After abandonment, the number of woody species increased significantly to twenty-eight, whereas the herbaceous species declined. After 3 years, the total number of woody species was 90% of that in the undisturbed forest. It is not expected that after this stage any more than three or four new species will establish.

The relative biomass and nitrogen, phosphorus, and potassium (NPK) accumulation levels in the undisturbed forest, cropping systems, and forest fallow are bimodal (Figure 8.2 a-d). At no stage are forest species completely absent. Earlier reports have discussed how sprouts from the stumps of cut trees are an important source of reestablishment and how they compete with crop species for water, space, nutrients, and light (Lambert and Arnason, 1986). If a site is only used 2 or 3 years for cropping,

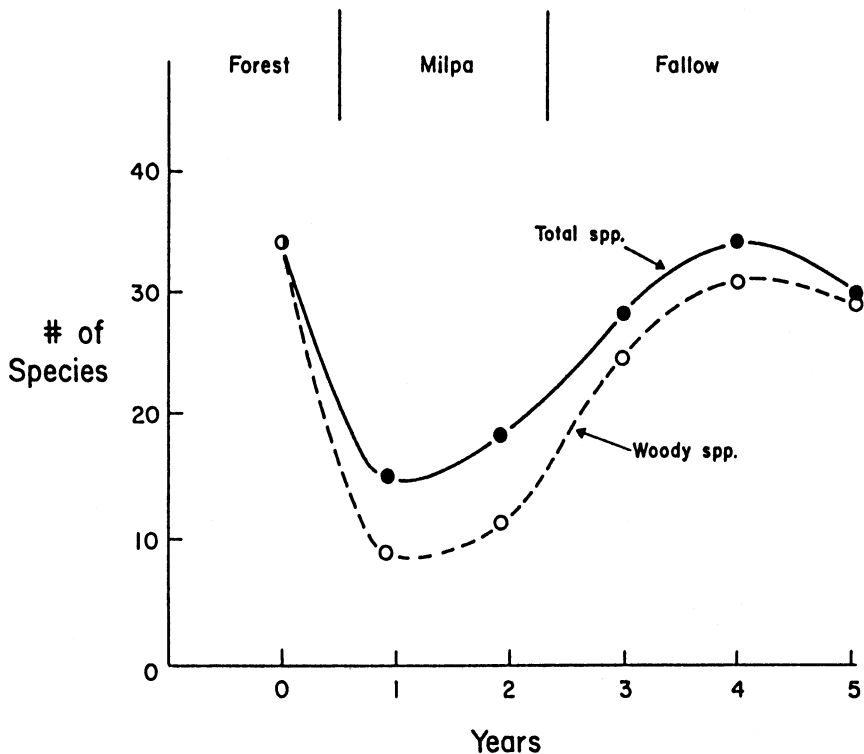


Figure 8.1. Number of woody and total species per hectare in the forest, milpa, and fallow period.

our evidence indicates that the original forest species are unlikely to be completely removed.

The presence of forest species contributes to the accumulation of retained biomass and nutrients. After 3 years of fallow, biomass is already 37% of the original forest, N is 50%, P is 31%, and K is 57%. Although crop harvest is responsible for a significant loss of nutrients from the plant nutrient pool at the site, the rapid recovery of forest conditions is in great part because of the base-rich soil present in the region.

Herbs and herbaceous vine life-forms have a very short existence in the forest fallow. The openness of the site after cropping affords ideal conditions for their establishment and rapid growth. Within 3 years though, they are no longer considered an important component. However, their dominance during the initial stages of succession makes up a far greater share of the nutrient pool than that of the woody species.

A further examination of the percentage of NPK in leaves and accumulating woody growth of trees, shrubs, and woody vines shows that during the cropping years and first year of fallow, nutrient concentrations are higher than in the undisturbed forest (Figure 8.3 a-c). The data show

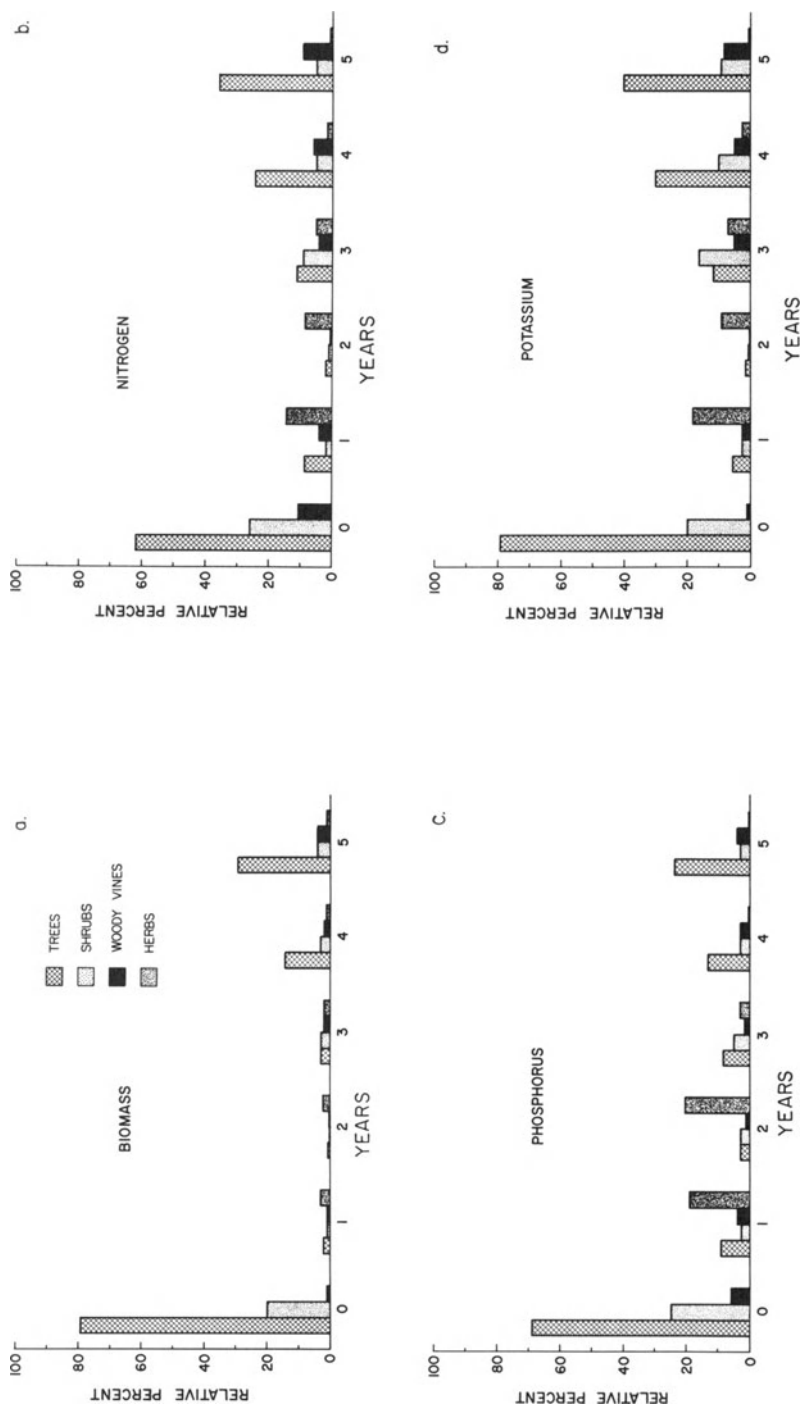


Figure 8.2 (a-d): Relative biomass and NPK in trees, shrubs, woody vines, and herbaceous species for forest, milpa, and fallow periods. Year 0 = undisturbed forest; years 1 and 2 = cropping period; years 3, 4, and 5 = fallow.

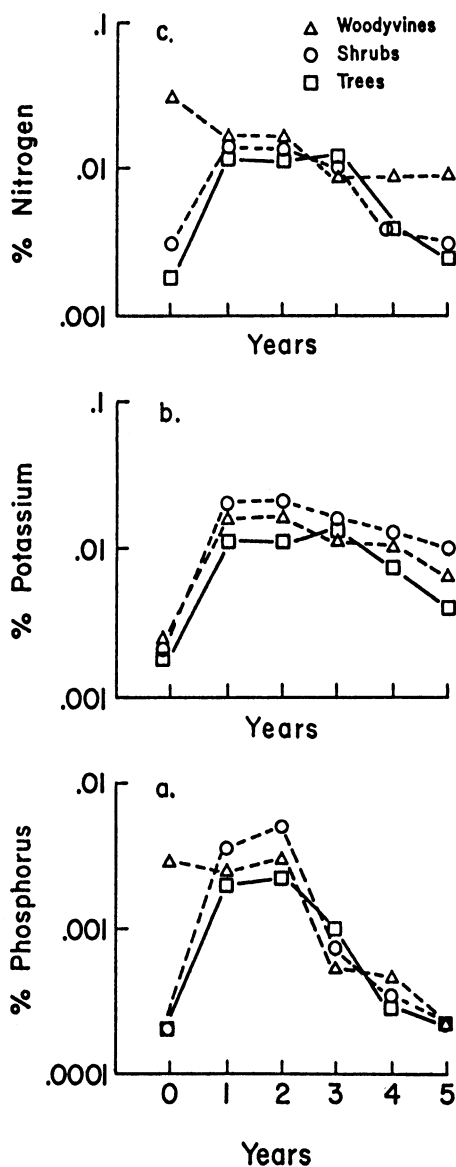


Figure 8.3 (a-c): Percentage of NPK in leaves and woody components of trees, shrubs, and woody vines for forest, milpa, and fallow. Year 0 = undisturbed forest; years 1 and 2 = cropping period; years 3, 4, and 5 = fallow).

a similar trend to that reported by Bartholomew et al. (1953) for 2-, 5-, 8-, and 17-year forest fallow in Zaire. This situation again reflects the increasing accumulation of wood biomass and reduction in leaf biomass as a percentage of total plant biomass. By the third year of fallow, nutrient

Table 8.1. Leaf to wood biomass ratio and nutrient concentration ratio following clearing and cropping of the original forest at Indian Church, Belize, CA

Land Use	Biomass	N	P	K
Forest	0.06	0.30	0.15	0.17
1st Yr Fallow	0.60	2.00	1.20	0.70
2nd Yr Fallow	0.30	1.10	0.70	0.50
3rd Yr Fallow	0.20	0.80	0.50	0.50

concentration percentages are not significantly different from those in the original, undisturbed High Bush forest (Lambert, unpublished data).

As long as the fallow period is sufficient for reestablishment and growth of forest species, they can be expected to contribute to nutrient recovery after cropping. If the cropping period is extended beyond 2 or 3 years, annual burning might be expected to reduce woody species to extremely low numbers in the agroecosystem. Their reintroduction would then have to come from sources external to the fields, taking much longer for full reestablishment.

An effective means of conserving nutrients in tropical forest systems is by their accumulation in wood biomass. In the initial stages of forest fallow, the ratio of leaf to wood nutrient concentrations is high. The rapid turnover of leaf biomass relative to wood biomass leads to a higher rate of uptake of stored nutrients in the wood. As the trees increase in height and girth, the ratio of leaf to wood decreases with the corresponding increase in immobilized nutrients.

Data in Table 8.1 show how rapidly the ratios drop within the first three fallow years, an indication of a significant increase in wood biomass. However, because leaves are constantly falling and being replaced, they are associated with a large, mobile nutrient pool. An examination of litter over a 12-month period showed that of the total N present in the forest system, 43% was in the leaves, as was 39% of the P and 25% of the K (Lambert and Arnason, 1980). Although the ratio might be low at any time, the leaves are nevertheless an important source of mobile nutrients.

The recent discussion by Saldarriaga (1986) of nutrient accumulation in forest succession following shifting cultivation near San Carlos de Rio Negro, Venezuela summarizes data in ten-year categories. Figures for N, P, and K suggest that leaf levels exceed wood levels for the first few years, and that woody biomass is greater than leaf biomass from the beginning. The problem with such data is that little if any information can be inferred concerning what is really happening during the first few years of abandonment regarding nutrient mobility.

Analysis of the litter in the undisturbed forest showed that there was essentially no removal of either P or K before leaves were shed, a con-

dition observed by Cole and Rapp (1980) for temperate deciduous forest species, where N withdrawal was approximately 40% before shedding.

Species that establish in the initial stages of the fallow, in what we consider to be a fertile site, would be competitive and ruderal species (Grime, 1979). The woody species with their high root-absorption capacity can exploit the unshaded habitat more readily than the herbaceous species with a low root-absorption capacity. It is only when the agricultural stage is prolonged and weeding occurs that the well-established herbaceous stage inhibits the rapid return of woody species (Kellman, 1969; Toky and Ramakrishnan, 1983).

8.3 Conclusions

The destruction of the nutrient-cycling ability of forest ecosystems with the imposition of a short agricultural cycle can be followed by a rapid recovery of the forest. Providing the root systems of the original forest species have not been destroyed, woody-species dominance is quickly achieved. The high base condition of the soil substrate in this Belize site ensures that all elements are readily available. Between the first and third fallow years, NPK accumulation in woody tissues doubled, and N and K were slightly in excess of the 50% levels in the 45-year-old forest. Although the accumulation rates will probably slow as the fallow ages, it could be expected that these sites could be used every 7 to 10 years for cropping.

Foliar uptake rates have not been directly measured for tree leaves in forests (Parker, 1983). Few studies have examined the role that increased litter fall plays in nutrient cycling at this early stage. The short lived leaves and actively growing green woody stems play a crucial role in nutrient uptake and transport.

The system of nutrient dynamics presented above indicates the aggressive character of fallow (successional) species. Limitations to the data are evident. An examination of the nutrient content of leaf litter and living leaves throughout the growing season would give useful information on availability, uptake, translocation, and immobilization of essential elements. In addition, data on the role of environmental parameters (e.g., precipitation, temperature, increasing shading, insect herbivory, etc.) would give a better understanding of the system.

Such studies urgently need to be expanded to understand the limits and possibilities for sustainable management of forest/fallow systems. Each site and region has its own particular combination of ecological and cultural conditions, and an agroecological approach is needed to balance the needs of farmers in these areas and the ability of their agroecosystems to meet those needs.

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9. Low-Input Ideotypes

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9.1 Introduction

Breeding for a given idealized crop model fitting into a high-input agroecosystem has been strikingly illustrated by the wheat ideotype of Donald (1968).

Beachell and Jennings proposed a similar crop model (1965) and so contributed to the success of the recent rice varieties of IRRI (International Rice Research Institute, Los Banos). The development of theoretical plant ideotypes should turn the erratic process of breeding for isolated features like “yield” or “defect elimination” into a systemic approach that integrates the whole plant into its ecology and its yield-related factors. Up to now, ideotype breeding has been tailored to a modern, high-input agroenvironment. Donald (1968) designed his basic wheat ideotypes for well-fertilized fields with adequate water supply (Figure 9.1).

In the tropical areas, the breeder generally faces low-input agricultural practices, except for labor (Swaminathan, 1979; Bouharmont, 1980). The success of high-input varieties in developing countries has been restricted to a few privileged areas. Many of the high-input varieties, selected under the favorable conditions of research stations, failed at the farmer’s level (Jurion and Henry, 1967; Glaeser, 1977). The failures of high-input varieties on tropical farmland has resulted mainly from the ecological and economic situation of these areas. It is generally admitted that the humid part of the tropics has an ecological disadvantage, particularly in terms of durable soil fertility, resulting in very low fertilizer response (Weischet, 1977; Rutunga and Neel, 1980). King (1979) estimates that 65% of the

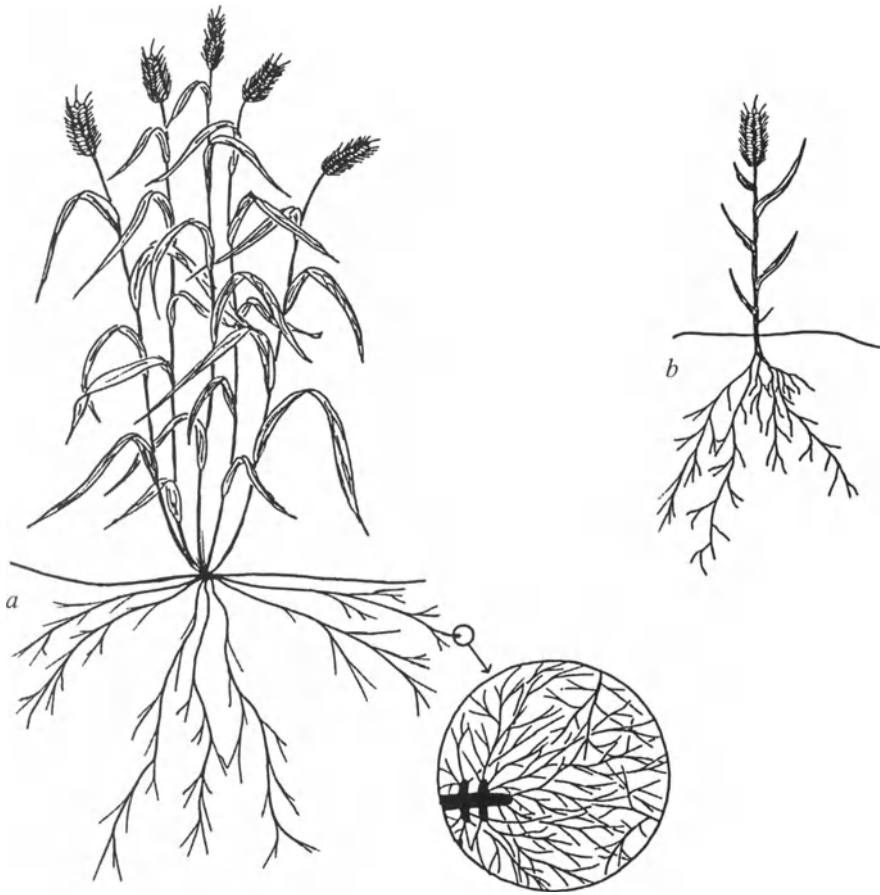


Figure 9.1. Schematic representation of a low-input ideotype (a) and a high-input ideotype (b). (After Donald, 1968).

tropical area is ecologically fragile. Yet, 35% of the world population lives in this fragile area, where development standards are lowest, and where malnutrition and hunger are commonplace. The introduction of high-input technology in such areas is hampered by a series of near insurmountable constraints, from the national level down to the farmer. Considering that the productivity of many farm areas in the tropical belt is stagnating or even decreasing (Meerman and Cochrane, 1982), and that most of the relatively fertile soils in the tropics are already under cultivation, there is an urgent need to develop new, input-saving technologies. This would bridge the gap between the vital need for higher productivity of the farmland on the one hand, and economic and ecological constraints on the other hand. The main traits of such low-input technology were defined by Gliessman (1977), Egger (1978), and Sachs (1980) as follows:

1. External production inputs should be low, and should only be used if a high efficiency rate can be secured.
2. Priority should be given to the use of locally obtainable resources.
3. The conservation of natural resources and their sustained use have to be guaranteed.
4. Technologies have to be adapted to the sociocultural setting of the population.

Research work with multiple cropping systems (American Society of Agronomy [ASA], 1976), recycling of organic wastes on the farmland (Prasad et al., 1974), multistory farming (International Council for Research in Agroforestry [ICRAF], 1980), and nitrogen supply by the Azolla fern, illustrate possible ways of implementing low-input technologies.

As advances in plant breeding contributed tremendously to the increase of productivity in high-input agriculture of the temperate zones during the last 100 years, the authors believe that it could fulfill a similar contribution in the tropics in the frame of a low-input strategy. First steps have already been undertaken by Jain (1977), Buchting and Elmheuser (1978) and Bahl (1980) by proposing a plant model that would suit a transitional type of agriculture in the following ways: high tillering capacity should be encouraged in cereals, a high potential for branching should be adapted in legumes, and finally, high yields should result both from a high harvest index and a high biological yield. Turner (1981) has designed plant models for dryland farming, and Francis (1979) proposed the development of plant genotypes for multiple cropping systems.

The long domestication of crop plants, which began over 10,000 years ago, has been an input-limited process up to the last century, except for labor, manure, fallow, irrigation water, and draft animals. It is only from the 20th century onward that selection has been applied under high-input conditions. Domestication has been a disruptive selection process in that cultivated plant types have become increasingly differentiated from the concurrent wild types (Harlan, 1975). Domestication of crop plants has been a combination of deliberate choices by man together with implicit correlated modifications, such as nonshattering, more determinate growth, increase in percentage of seed set, inflorescence size and number of inflorescences, and reduction of sterile flowers. Selection pressure for better seedling competition has resulted in greater seed size, lower protein and higher carbohydrate content, loss or reduction of germination inhibitors, and reduction in glumes and other appendages (Harlan, 1975). Dwarfing of crop plants has resulted in smaller root systems, and hence in decreased numbers of mycorrhizae. In the face of this selection and global distribution of the germplasm, preservation of the genetic variability within crop species has become a major concern in recent years (Frankel and Hawkes, 1975; Feldman and Sears, 1981).

The present chapter will attempt to describe a general, theoretical, low-input ideotype that would fit into a low-input agroenvironment. Partic-

ular attention is directed to the humid tropics where cultivated crops are believed to retain a higher proportion of ancestral characteristics than those found in temperate zone populations. The low-input ideotype should integrate this diversity.

9.2 The Target Area

The design of a low-input ideotype implies identifying, both on a regional and local basis, the host agroenvironment, and more particularly, the available resources.

9.2.1 The Host Region

In the humid tropics, because of strong demographic pressure, sedentary forms of agriculture are steadily replacing traditional types of shifting cultivation or semipermanent cropping (Jurion and Henry, 1967). Soil fertility, which used to be adequately recovered during periodical long-term fallows, is now progressively vanishing. The intensity of soil degradation is such that Farnworth and Golley (1973), and King (1979) have labeled the humid tropics as "fragile ecosystems." Many soils in the humid tropics are characterized by two-layered clay minerals with weak adsorption capacity (Mohr et al., 1972; Weischet, 1977). High temperature and humidity accelerate the degradation process. The cation exchange capacity (CEC) generally is lower than 15 meq/100 g of soil, and the saturation (V) is lower than 30% (Neel et al., 1976). Hence, the use of water-soluble mineral fertilizers will result in a high rate of leaching. Soil structure itself is often inadequate, resulting in a higher erosion rate, weak water-retention capacity and a reduction of gaseous exchanges.

Yield increases from mineral fertilization often do not justify the expense. The limited capacity of developing countries to produce agrochemicals and agricultural equipment results in the expensive import of production means, the amount of which will be necessarily limited by available foreign exchange.

9.2.2 The Target Farm

At the farmers' level, the situation becomes even worse, as most farmers in the tropics are small holders, except for the *latifundist* and the plantation type of agriculture. In Rwanda and Burundi (Africa) the great majority of the farms are between 0.5 and 2.0 ha. To resaturate to CEC the top 30 cm of an average soil (CEC = 15, V = 30%) in these countries would require not less than 3500 U.S. dollars/ha of imported Potassium chloride (KCL) fertilizer with locally available lime (150 U.S. dollars/metric ton). No small farmer can afford this, considering that the average yearly income per inhabitant is less than 200 U.S. dollars (Barney, 1980).

9.2.3 The Output/Input Ratio

The output/input energy ratio can be as low as 0.2 in highly mechanized agriculture, whereas it can reach values up to 40 to 50 in food gathering agriculture (Evans, 1975). The caloric output/input ratio of maize cropping in the U.S. has decreased from 3.7 in 1945 to 2.82 in 1970 (Pimentel et al., 1973). If input prices continue to increase faster than output prices (Barney, 1980), then high-input farming will become less and less profitable, because of a decreasing efficiency of input valorization.

9.2.4 An Ecologically Adapted Strategy

Clearly there is a need to implement a development strategy that fits the ecological and socioeconomic constraints of the problem areas within the tropics. The following concerns must be addressed by such a strategy.

9.2.4.1 Resources

A limiting production factor in the humid tropics is the provision of adequate nutrients to the system. Before deciding to introduce mineral fertilizers into the small-holder's system as external input, priority ought to be given to methods that improve the use of the following *in situ* resources:

- Mineral nutrients from the deeper soil layers
- Atmospheric nutrients, particularly nitrogen
- Immobilized phosphorus reserves in the soil
- Manure, compost, or mulch, either by recycling or by external input to the field.

9.2.4.2 Losses

The exploitation of available nutrient reserves implies that nutrient losses from the farm should be minimized if productivity is to be maintained. The principal nutrient losses, apart from yield exportations, are from leaching, erosion, fixation of elements, and inappropriate recycling of organic wastes. The farm system needs to ensure an expanding pool of nutrients that would be readily available for the crops.

9.2.4.3 Storage of Nutrients

The low CEC of most soils in the humid tropics can be raised by increasing both the organic matter and the humus content. The CEC of organic matter ranges from 150 to 500 meq/100 g organic matter (Weischet, 1977). Unfortunately, organic matter breaks down rapidly in the humid tropics. Hence, the most practical way of storing nutrients under such conditions is through "standing biomass." In humid tropical ecosystems, total nutrient content is positively correlated with total biomass

(Weischet, 1977). The productivity of a low-input system is based on the degree of internal biomass circulation, of which only a part is taken for actual yield production. Hence, a large biomass pool should be built up and rapidly turned over, so that equilibrium is maintained in the soil between buildup and breakdown of the organic matter, while ensuring a substantial increase of the CEC. This in turn will allow application of water-soluble nutrients like mineral fertilizers (Egger, 1978).

Soil structure, water retention capacity, and erosion control are of paramount importance for the efficiency of nutrient cycling. Plants as standing biomass will contribute to stabilization of microclimate and reduced erosion and organic breakdown. Thus organic matter content, water-holding and biological activity of the soil will increase as well.

9.2.4.4 Forms of agroecosystems

As opposed to conventional monocropping systems, a low-input strategy designs agroecosystems with high structural and species diversity to exploit local nutrient resources, prevent nutrient losses, and protect crops and soil fertility. Numerous ecologically suitable agroecosystems, based on a well-developed biomass during the largest part of the year, are found throughout the humid tropics. Such systems combine different species, ordered or mixed in space and time, and perennial crops, often coexisting with seasonal crops under multi-story farming (ICRAF, 1980; ASA, 1976; Institut de Sciences Agronomiques du Rwanda [ISAR], 1979). Within the same species, varietal mixtures are frequent. The biomass pool of such systems is reinforced by the complementary and mutually beneficial effects of compatible species combinations (ISAR, 1979). Clearly, breeding for such low-input environments implies selecting genotypes that produce a large amount of biomass, and withstand strong intergenotypic and interspecific competition.

9.3 The Biomass Bank

A large root system reaching deeper soil layers will enhance acquisition of mineral nutrients. Assimilation of atmospheric nutrients will be improved by a profuse and active biomass. Buildup of organic matter in the soil will, of course, be proportional to the total amount of biomass. In turn, a high organic matter content of the soil will increase the efficiency of possible applications of costly mineral fertilizers and/or lime. Consequently, yield will be biomass dependent not only in the short run, but even more so in the long run.

The senior author compared twenty-nine clones of sweet potato at 150 days of growth for leaf area index (LAI) and for dry matter production of roots, vines (without leaves), and leaves. The biomass (BM) was de-

Table 9.1. Correlation matrix between six yield-related traits in 29 clones of sweet potato

	Leaf Dry wt	Vine Dry wt	BM ^a	HI ^b	LAI ^c
Root Dry wt	-.07	-.04	.73**	.83**	.04
Leaf Dry wt		.33	.53**	-.39**	.74**
Vine Dry wt			.50**	-.36*	.44*
BM				.33	.54**
HI					-.20

^a Biomass Index (BM) = dry weight sum of roots, vines, and leaves.

^b Harvest Index (HI) = ratio of root weight to biomass.

^c Leaf Area Index (LAI) = an index of canopy layers.

* Statistically significant at $p < .05$

** Statistically significant at $p < .01$

fined as the dry weight sum of roots, vines, and leaves. The harvest index (HI) was calculated as the ratio of root weight over biomass. The correlation matrix for these six traits is given in Table 9.1. The strong positive correlations of root dry weight with BM ($r = 0.73$) and HI ($r = 0.83$) give further support to the model proposed by Jain (1977). Both BM and HI are strong yield contributors. Leaf and vine dry weight both contributed to the biomass buildup ($r = 0.53$, $r = 0.50$, respectively). However, LAI did not contribute directly to the root yield ($r = 0.04$), although good correlation was found with biomass ($r = 0.54$). This may indicate that most clones are sink limited, as suggested by Hahn (1977), or that the late-maturing clones (i.e., primarily the clones with high LAI) do not reach full tuberization by 150 days.

Low-input ideotypes will have a high amount of “standing” biomass, which will permit storing nutrients as long as agronomically possible, i.e., the entire crop season, and reducing the mineralization rate of organic matter in the soil by providing an adequate leaf canopy. In a low-input ideotype, the whole plant will be considered a sink, or a biomass bank, from which only a small part will be diverted into the agronomic yield sink and exported from the farm system, the bulk being recycled. Among the best yielders, the breeder will prefer an ideotype with high biomass and low harvest index, a combination that maximizes remaining harvest residues at a defined level of yield exportation from the farm system. Growth cycles, and more importantly seed-filling periods or tuberization processes, will be kept as long as possible by choosing indeterminate types, insofar as the agroenvironment triggers the maturation process. If not, semideterminate types will offer a good compromise. Determinate types will only be used whenever definite time requirements have to be met, as in the case of a snatch crop, or pathogen/pest avoidance. Moreover, it should be noted that there are many cases where short-cycle crops have the advantage of permitting a second or even third crop per year—re-

sulting in a large total annual biomass. A low-input ideotype will be considered efficient insofar as it has a high rate of total dry matter production per unit area, unit time, unit of external input, and unit of output (yield exportation). If a crop failure would occur, a low-input ideotype would at least leave some biomass behind.

9.4 Environmental Adaptability

A low-input ideotype should be adapted to fit into a particular physical and climatic environment with seasonal variations, i.e., into an agroecological niche. Adaptability should be specific with regard to site and climate, and large when it comes to coping with the seasonal weather variations, as well as the microsite variations (Table 9.2). Grafius (1965) states in his fifth law that it is always possible to find a variety with equal or better yields in a specific environment than the universal variety. This law has been confirmed in two series of multilocal and multiseasonal trials of sweet potato, led by the senior author in Rwanda (ISAR 1980, 1981). A broadly adapted variety (Rusenya) was usually outyielded in a specific site by a site-specific variety. In a first series comparing nineteen clones, Rusenya was outyielded in eleven of fourteen environments, although it was the overall best variety (ISAR, 1980). In the second series comparing thirty clones, Rusenya was outyielded in fifteen of sixteen environments, although it was the second-best yielder overall (ISAR, 1981). Hence, taking the mean of a variety trial in a given site as representative of the site index is questionable. Evenson et al. (1978) prefer to take the yield of the highest-yielding variety in a given site as representative of that site index. Consequently, yield stability across environments can only be achieved at the expense of some yield losses in most of the specific environments. Breeding for adaptability towards a broad spectrum of climates, microsites, and agroenvironments becomes an idle exercise unless (1) particular qualitative, industrial requirements have to be satisfied; or (2) the germplasm base of the presently cultivated population is extremely narrow, such as is the situation with maize in East-Central Africa. Low-input ideotypes will be grown in environments where

Table 9.2. Environmental adaptability characteristics of low-input ideotypes

	Type of Adaptability	
	Specific	Unspecific (wide)
Site		Microsite
Climate		Seasonal variations
Cultivation practices (agroenvironment)		Bioenvironment

external inputs like manure and mineral fertilizers will be so limited that they will not be able to correct for mismatching between genotype and environment. For each specific environment, a specific genotype will have to be bred. The following proposition can be forwarded. Each low-input agroecological niche requires a specific low-input genotype.

The apparent contradiction between specific and wide adaptability could be overcome by attaining specific adaptation for site, climate, and agroenvironment, at the group (family, progeny) level, while allowing for large within-group (among individuals) adaptation for microsite, seasonal weather variations, and bioenvironmental changes. Allogamous species could be tested for environmental adaptability by multisite and multi-seasonal trials of heterozygous structures (families, synthetic populations, land races). With inbreeding crops, it will be more difficult to overcome this contradiction. However, interest is growing in providing self-pollinating species with heterogeneous, if not heterozygous, structures at the release stage, for instance, by stopping the selfing series at the F3 or F4 generation, as soon as a reasonable phenotypic homogeneity has been reached (Lerner, 1954), or by producing hybrid varieties, as is presently attempted with hybrid wheat (Zeven, 1979). Multilines or variety mixtures are interesting examples of reaching this contradictory objective. Both in Rwanda and Burundi, good results have been obtained so far with mixtures of bush bean varieties, whereas mixtures of climbing beans were not found to be more advantageous than pure lines (Nyabyenda & Mpabanzi, 1980; Institut des Sciences Agronomiques du Burundi [IS-ABU], 1982). This latter finding is not surprising because the indeterminate nature of climbing beans gives them more adaptability potential against microsite, weather, and biotic variations than bush beans (determinate type).

Breeding for low-input ideotypes should also concentrate on gathering all possible desirable alleles commanding high yield potential under low-input environment, and conversely, on either getting rid of, or at least neutralizing, all unnecessary alleles that are known to depress yield potential. The importance of short stature and/or early maturity should be regarded critically within a context of the concerned farming system, because both these traits are generally negatively correlated with yield. Presently, most wheat breeders have relaxed their dwarfing objective, as semidwarf cultivars have been found to be a far better compromise between lodging resistance and yield potential (Gale & Law, 1977). Similarly, breeding for a large, grain-crop seed size will generally result in yield depression, as well as higher seed rate (weight wise). The breeder facing low-input target areas should not become dogmatic about rejecting all so-called unnecessary traits. He or she should be satisfied with aiming at yield potential under low-input environments, while avoiding putting any selection pressure either for or against any of these unnecessary traits, and hence conceding progress (or regression) of these traits.

One kind of adaptation is the specific one arising toward a given agroecological, low-input environment, which results from local cultivation practices. In many cases this implies adaptation for a rough sowing bed, competition against weeds, and good storage ability, as well as the potential to sustain competition in variety mixtures, mixed crops, and intercropping stands (ASA, 1976; Francis, 1979). Intercropping studies should consider not only the best combinations among species, but also the best reciprocal varietal arrangement among species (ISAR, 1981).

9.5 The Root System

9.5.1 The Structure of the Root System

Roots are the foundations of plants, and yet they remain relatively unknown, compared to the rest of the plant. MacKey (1973) points out that one of the dwarf wheat varieties that contributed so much to the green revolution happened to be Pitic 62, which is characterized by an exceptionally large root system. According to him, seminal root systems in wheat are preferable to the crown type of root system. Water uptake of the seminal rootlets has been found to be more efficient in pot experiments (Passioura, 1972). The theoretical maximum number of seminal rootlets is ten (MacKey, 1980). Under field conditions, however, it seems pointless to restrict the root system to the seminal system. Unless there exists a strong, well-developed, complementary, crown (nodal) root system, plants are unable to exploit the numerous small rains, common in the seasonal tropics, that wet only the upper 5 to 10 cm of soil. Top-soil roots are also known to be very important in recycling the above-ground organic matter (Gliessman, 1977). Low-input ideotypes should therefore possess a dimorphic root system, as is the case with gum trees, i.e., a very deep tap-root system beyond topsoil depth, combined with a very wide and dense shallow-root system (Figure 9.1). A strong root system will enhance the pedogenetic process by weathering the subsoil. Moreover, it will better withstand occasional water shortages, as well as competition with other varieties, intercropped species, and weeds. Low-input ideotypes for the dry tropics and subtropics will, of course, be characterized by a higher root/shoot ratio. As for the symbiotic uptake of nitrogen by legumes and some nodulating species (Vlassak, 1972), one should attempt to breed for a higher efficiency of the symbiotic mechanisms (Riley et al., 1979). A good example of this is given by the soybean-breeding work of Kueneman (1981), where promiscuous nodulation is an objective.

9.5.2 Mycorrhizae

Most cultivated plants and forest trees have roots associated with symbiotic, beneficial fungi that increase nutrient and water uptake and may

protect the root from certain diseases. These infected roots are called mycorrhizae. In a low-input system, they are most important in improving phosphorus nutrition. Phosphate is generally present in the soil in low concentrations, and is also highly immobile. Strands of fungal hyphae grow out from mycorrhizae and increase the volume of soil from which phosphorus can be obtained. Hence, mycorrhizal plants in general can grow and thrive in soils much lower in phosphate and other nutrients than a comparable nonmycorrhizal plant. Many plants are so dependent on mycorrhizal fungi for nutrient uptake that they may starve if these fungi are absent. Mycorrhizae are particularly important for many N-fixing plants and trees, in that they stimulate nodulation by symbiotic bacteria, thereby increasing nitrogen fixation. Improved phosphorus nutrition of the mycorrhizal N-fixing plants is responsible for increasing nodulation. Mycorrhizae of agricultural crops are not host specific. Thus the same fungus producing mycorrhizae on many tropical tree species will form mycorrhizae on agricultural crops. So agroforestry systems will ensure inoculum production by trees. If soil is treated with fumigants to kill pathogens, mycorrhizal fungi are also killed, and considerable time is required for them to become reestablished naturally. The nutrient deficiencies and associated stunting that often result may be prevented by inoculating the soil with mycorrhizal fungi rather than by applying excessive rates of fertilizers. The greatest opportunity for the use of mycorrhizal fungi is in soils low in available phosphorus, including many untreated soils in tropical regions. There is evidence that many of these soils also contain less than the optimum number of propagules of mycorrhizal fungi (National Academy of Sciences, 1979).

Several American commercial companies are interested in producing pure inoculum of selected mycorrhizal fungi. An inoculum for tropical pines is already available (Marx et al., 1982). Pines cannot grow beyond the first year without an appreciable number of mycorrhizae. Because inoculum may be produced by small-scale methods instead of industrial procedures, this technology can be introduced into developing countries. The fungi that form mycorrhizae on pine are truffles, mushrooms, and puffballs. The puffball fungi usually contain an abundance of easily extractable spores. For example, one fruit body of *Pisolithus tinctorius*, which is the fungus selected for commercial production in the U.S.A., may contain more than 75 billion spores. In Rwanda, *P. tinctorius* is abundant in fast-growing plantations of eucalyptus, suggesting that the fungus is ecologically adapted to most parts of the country. Unfortunately, the physiological races symbiotic to pine are absent. Current research at the Forestry Division of ISAR aims at introducing that inoculum from the U.S.A. and reproducing it in the country. At ISAR, vigorous *Pinus patula* seedlings were obtained on eroded oxisol after treatment with *P. tinctorius* spore suspension and no fertilizer.

Until now plants have been bred for their response to fertilizers rather than for their symbiotic properties. One of the most inhibiting factors to mycorrhizal infection is heavy fertilization. In turn, the plant can only use fertilizers efficiently when strongly mycorrhizal. Another important inhibiting factor is irrigation. Conversely, roots can better stand drought when mycorrhizal. Fungicides can kill pathogens as well as mycorrhizal fungi. However, mycorrhizal roots are less vulnerable to pathogens. Eradication of rodents and insects feeding on mycorrhizal fungi can deter the most important propagation vectors of mycorrhizal fungi.

Marx and Bryan (1971) suggested that host genotype controls the benefit seedlings obtained from certain ectomycorrhizal relationships. Moreover, the enhancement of growth due to ecto-mycorrhizal formation on *Pinus contorta* seedlings was strongly influenced by host seedling genotype (Cline and Reid, 1982). The correlation between total dry weight and mycorrhizal infection percentage within *P. tinctorius* treatments suggested that the benefit *P. contorta* seedlings received from mycorrhizal associations is controlled directly by the amount of infection. Of course, host genotype had an indirect effect by influencing the degree of mycorrhizae development on seedlings. No single mycorrhizal fungus was universally superior in growth improvement or mycorrhizae formation among all seed sources, because both seed source and fungal species determined growth response. Therefore, Cline and Reid (1982) conclude that consideration must be given to tree species, seed source, and fungal species used for inoculation to ensure optimal seedling growth. Consequently, low-input ideotypes should have efficient mycorrhizal association.

9.6 The Low-Input Ideotype

In Table 9.3 and in Figure 9.1, the most striking traits of a low-input ideotype are contrasted with a high-input ideotype suggested by Donald (1968).

9.7 Conclusions

Breeding for low-input ideotypes should not be regarded as a romantic return towards the ancestral wild plant type, but rather as an effort to produce a plant model that would fit into a biomass-oriented agroecosystem and which would match the low-input conditions prevailing in most of the humid tropics. This low-input ideotype should combine the well-explored variability of cultivated genotypes with the available but underexplored variability of the vanishing wild gene pools. Although this plant model is proposed for the humid tropics, it is believed to be extendible, after a few modifications, to low-input ideotypes for the dry

Table 9.3. Traits of high- and low-input ideotypes

Character	High-input ideotype	Low-input ideotype
Biomass		
Amount	Small	Large
HI ^a	High	Rather small
LAI ^b	About 3	Higher than 3
Tillering	Uniculu	Heavy tillering potential
Stem Size	Dwarf	Tall
Branching (dicots)	Little	Multiple
Productivity	Yield/area/time	Biomass/area/time and external input
Environmental adaptability		
Site	Wide	Specific
Climate	Wide	Specific
Microsite	Wide	Wide
Seasonal variation	Wide	Wide
Bioenvironment	Weak	Broad-horizon field resistance
Agroenvironment	Specific	Specific
Competitiveness		
Intergenotypic	Weak	Strong
With other crops	Weak	Good adaptation for intercropping
With weeds	Weak	Strong
Maturity		
Time	Early	As late as agronomically possible
Type	Determinate	a) Indeterminate if environment induces seedset or tuberization, otherwise, b) Semideterminate
Root system		
Structure	Seminal	Seminal, nodal (cereals) tap roots, shallow roots
Size	Confined to top soil	Deep (others), widely spread out
Bacterial and/ or mycorrhizal associations	Inefficient	Efficient
Seed		
Size	Large	Rather small
Number/ear	High	High
Rate	High	Low (weightwise)
Genetic structure		
Inbreeders	Pure lines	Multilines, varietal
Outcrossers	Hybrids	Mixtures (synthetic) populations

^a Harvest Index (HI) = ratio of root weight to biomass.^b Leaf Area Index (LAI) = an index of canopy layers.

tropics and subtropics, and even for the energy-conscious temperate agriculture.

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10. An Ecological Approach to Reducing External Inputs Through the Use of Intercropping

M.F. Amador and Stephen R. Gliessman

10.1 Introduction

Resources that promote plant growth in agroecosystems, such as light, water, and nutrients, contribute to the formation of biomass, a part of which eventually leaves the system in the form of harvest yields. A major concern of agriculture has been how to maximize this output of biomass, with much research focusing on the development of optimal crop densities, which promote the most efficient uptake and conversion of these resources into profit-producing yields. In conventional agriculture, though, this focus has used primarily single-crop plantings, where it is possible to maintain optimum fertilizer levels, water availability, and light capture, as well as keep other factors at levels that are of benefit to the crop output. With additional inputs for weed, disease, and insect control, sole-crop planting systems can achieve substantial yields and profit. But as awareness of the combined ecological and economic costs of maintaining yields in these monoculture systems has grown, the search for alternatives that rely less on fossil-fuel based energy and material inputs has begun to intensify (Altieri, 1987; Stinner and House, 1988). One of these alternatives is intercropping (Francis, 1986).

Intercropping is an intensified form of multiple cropping, where two or more crops are grown simultaneously on the same land (Andrews and Kassam, 1976; Gliessman, 1985; Francis, 1986). Crop intensification is in both the time and space dimensions of resource availability, with the

accompanying potential for interference between the crop components during all or part of the growing season (Trenbath, 1976, 1986; Vandermeer, 1984). Because this interference can have both positive and negative impacts on biomass production and harvest yields, it is important to gain an understanding of the ecological basis for the interactions (Gliessman, 1986). Such knowledge will determine, to a great extent, if the intercrop system will be successful in maintaining or improving yields, as well as lowering the need for external inputs for its management.

10.2 Ecological Advantages of Intercropping

In many areas of the world where intercropping is a common component of agroecosystem management, it has often been shown that there can be definite advantages to planting crops together in the same place at the same time (Kass, 1978; Willey, 1979; Gliessman et al., 1981; Francis, 1986). Farmers are often able to achieve a greater total production on their land with the mixtures than if their land were divided and planted to a combination of monocultures. In some cases, yields of some members of the crop mixtures may be stimulated, and in other cases there may be slight reductions, but the combined yield of the intercrop on less total land area is the important aspect. It is very important to gain an understanding of the ecological mechanisms of yield increases in order to take better advantage of the use of intercropping systems (Gliessman, 1986).

In a well-known study by Trenbath (1974), the results of 572 crop mixture experiments demonstrate that the majority (66%) had a combined yield total in the mixed plantings that was no different than the sum of equivalent areas planted to the monocultures. On the other hand, when the yields for each crop planted in a mixture was divided by its yield in monoculture, and then each of these values summed for all of the crops in the planting (a value known as a Land Equivalent Ratio—LER), 20% of the combinations gave values greater than 1.0, with some ranging up to 1.7 (Figure 10.1). These cropping systems indicate that there were distinct advantages to planting the mixtures. The 14% of the studies that gave LER's below 1.0 indicate that the combinations were at a distinct disadvantage as compared to the monocultures. It should be remembered that most of the cases reported by Trenbath were experimental systems, rather than actual farmer-initiated plantings. Farmers select systems that have shown advantage over time. A similar study of LER's of intercrop systems currently in use by farmers would undoubtedly show a high percentage of values above 1.0.

The fact that reports abound in the literature of intercropping systems that show advantage over monoculture plantings demonstrate the need for detailed research in order to take proper advantage of such systems as alternatives for the future. The first step in this analysis requires doc-

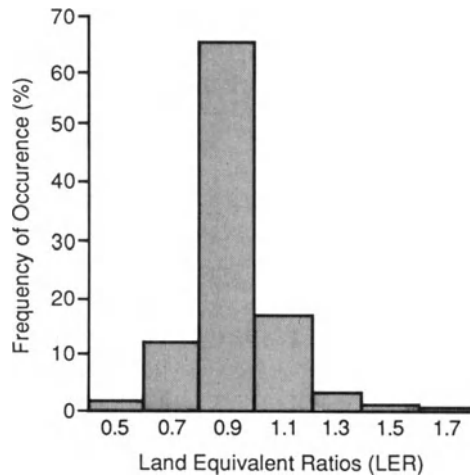


Figure 10.1. The distribution of Land Equivalent Ratios (LER) taken from 572 crop mixture experiments taken from the literature (adapted from Trenbath, 1974).

umentation of cases where overyielding (i.e., higher LER's in the mixtures) occurs. This can then be followed by detailed ecological and agronomic studies of the actual mechanisms that promote the better yields.

10.3 The Corn/Bean/Squash Intercrop System

One of the most frequently cited examples of an intercropping system that still enjoys widespread use and is thought to display distinct yield advantages is the traditional intercrop of corn, beans, and squash, commonly found throughout much of Latin America (Pinchinat et al., 1976; Amador, 1980; Davis et al., 1986). These three crops are planted in many different arrangements, sequences, and patterns, sometimes only two of them together, and at other times all three (Pinchinat et al., 1976; Laing et al., 1984). Data have been presented (Francis et al., 1976) showing that an average of 80% of the bean crop in many Latin American countries is grown in association with other crops. This percentage may have decreased somewhat in recent years in some countries, especially those where widespread technology transfer has occurred or where the costs and availability of labor may have increased, but it is highly likely that intercropping will persist for a long time as an important source of production of these staple food-crop items.

In order to gain an ecologically based understanding of one example of this system, an experiment was carried out at two sites with distinct

characteristics in Tabasco, Mexico, a tropical, lowland region of the country with a long heritage of traditional agriculture dating back to prehispanic times (West et al., 1969; Gliessman et al., 1981).

The first experimental site was on the grounds of the Colegio Superior de Agricultura Tropical (CSAT), near Cardenas, Tabasco, Mexico, and the other site was on land of the *Poblado C-34* (C-34), a community in the land-reform project known as the *Plan Chontalpa*. The second site was situated approximately 2 km southwest of the first. Soils in the area belong to the Limón Series and are grey to brown in color, with a clay to clay-loam texture (see Mejia, 1978, for detailed soil description).

The CSAT plot (8400 m²) was initially prepared with machinery, in accordance with the previous land use practices employed there. After plowing, discing, and furrowing, planting and crop care was the same as for the C-34 plot. The C-34 planting (4400 m²) has a history of use by local farmers, who employ a machete for the initial clearing, and then a pointed stick (*macana*) to make the hole into which the seed is dropped. Depending on the treatment, five seeds of corn, four seeds of beans, and three seeds of squash were used. The corn was a local three-month variety (*cuarentano*), the bean a local climbing variety of *Vigna* (*frijol sin tiempo*), and the squash a round-fruited variety of the local *Cucurbita* complex.

The distance between rows was approximately 1 m in C-34 and 92 cm in CSAT. The densities reported in Tables 10.1 and 10.2 were varied by means of increasing or decreasing the distance between holes planted in a row. Two densities (high and very high) above the polyculture density, and two (low and very low) below the polyculture density, were achieved. The four densities of beans were all higher than the monoculture density, due to recommendations from local farmers. They stated that the polyculture densities planted as monoculture would not make agronomic sense, so higher densities were used. We used these different plots to compare monoculture and polyculture densities, as well as to obtain the optimal monoculture response. A random block design with three repetitions was used for CSAT, and a modified Latin Square with four repetitions for the C-34. Plots were 6 by 8 m for C-34 and 10 by 9.2 m for CSAT. A 1 meter edge was eliminated during sampling for all plots. By including a weeded and non-weeded treatment for each density, a total of twenty-six treatments were employed. Total biomass (separated into harvestable portions of each crop) as taken, dried at 70 °C for 48 hours, and weighed. Agricultural yields were obtained as dry grain for corn and beans, and fresh weight of the fruits for squash. Land Equivalent Ratios (Vandermeer, et al., 1987) were calculated based on these yield data.

Site C-34. Comparing the yields of each crop at each monoculture density with both the weeded and unweeded polycultures, the highest corn yield was obtained in the weeded polyculture (Table 10.1). Of the monocultures the high-density planting achieved the highest yields, both for weeded and unweeded plots. Using the Analysis of Variance, no sig-

Table 10.1. Yields of the polyculture corn/bean/squash, compared with monocultures planted at 4 different densities at the C-34 site

	Monoculture Densities ^a				Polyculture
	Very low	Low	High	Very High	
Densities of corn	33,300.0	40,000.0	66,600.0	100,000.0	50,000.0
Yield with weeding (kg/ha)	990.0	1,150.0	1,230.0	1,170.0	1,720.0
Yield unweeded (kg/ha)	846.5	785.8	1,492.6	1,108.4	1,285.6
Densities of beans	56,800.0	64,000.0	100,000.0	133,200.0	40,000.0
Yield with weeding (kg/ha)	425.0	740.0	610.0	295.0	110.0
Yield unweeded (kg/ha)	140.0	122.0	344.0	438.0	75.0
Densities of squash	1,200.0	1,875.0	7,500.0	30,000.0	3,330.0
Yield with weeding (kg/ha)	15.0	250.0	430.0	225.0	80.0
Yield unweeded (kg/ha)	177.0	95.0	143.0	99.0	9.6

^a Densities expressed as number of plants/ha.

Table 10.2. Yields of the polyculture corn/bean/squash, as compared to monocultures planted at 4 different densities at the CSAT site

	Monoculture Densities ^a			Polyculture	
	Very low	Low	High	Very High	
Densities of corn	37,000.0	44,400.0	74,000.0	111,000.0	55,500.0
Yield with weeding (kg/ha)	470.0	430.0	835.0	790.0	262.0
Yield unweeded (kg/ha)	172.0	146.0	157.0	254.0	176.0
Densities of beans	62,400.0	73,600.0	108,800.0	148,000.0	44,400.0
Yield with weeding (kg/ha)	585.0	630.0	635.0	820.0	210.0
Yield unweeded (kg/ha)	382.0	441.0	614.0	482.0	128.0
Densities of squash	600.0	1,700.0	13,800.0	27,600.0	2,700.0
Yield with weeding (kg/ha)	237.2	22.7	0.0	0.0	0.0
Yield unweeded (kg/ha)	0.0	0.0	0.0	0.0	0.0

^a Densities expressed as number of plants/ha.

nificant differences were observed between the treatments, but a *t*-test comparing the mean yields of the monocultures and polycultures showed a significant difference at the 5% level. Bean yields were reduced considerably in the polyculture, when compared to the highest monoculture yield, which was achieved with the low density planting. Yields were uniformly reduced at all densities without weeding. The Analysis of Variance performed demonstrated significant differences between treatments. For squash, the high-density monoculture planting achieved the highest yield, being practically five times the polyculture yield. Without weeding, squash yields fell drastically in all cases.

In general, it can be seen that for the three crops the best yields were obtained with weeding: the greatest difference was observed with corn, where 490 kg/ha more grain was achieved than with the best monoculture. The unusually high yield for the unweeded, high-density corn monoculture is thought to be sampling error that cannot be traced, especially because for all other densities and crop species, the corresponding yields for the unweeded treatment were always lower than the yield from weeded treatment. Bean polyculture yield was the lowest of any density, partially because of the presence of the corn plants, but also because of its low density, compared to the monoculture densities. The planting density for the lowest-density monoculture surpassed the polyculture, due to recommendations by local farmers at the outset of the experiment on normal densities of monoculture bean crops. For squash, yields are very different with and without weeding, but variation from one treatment to another was very great. The small plot size was not great enough to accommodate the ranging habit of squash vines, thus many fruits were missed when only the experimental plot was harvested. In all cases, the coefficient of variation was very great, with 40% for corn, 59% for beans, and 101% for squash. This reflects the great variability often inherent in such systems.

Site CSAT. Yields in the CSAT site were different from the C-34 yields in many respects (Table 10.2). The highest yield for corn was observed not in the polyculture, but rather in the high density monoculture. Yields were considerably reduced by not weeding in all of the monoculture densities, and although reduced, yields were not reduced to the same extent by not weeding the polyculture. In fact, the yield differences between mono- and polycultures without weeding were not significantly different. Corn yields were generally much higher in the C-34 site than in the CSAT site, due to better soil conditions (Gliessman et al., unpublished data) in relation to nutrients and soil drainage.

Bean yields followed the same pattern as in the C-34 site, with unweeded plots consistently lower than the weeded plots, and polyculture yields being the lowest in all cases. The highest yield was obtained from the very high monoculture density. It is interesting to observe that the

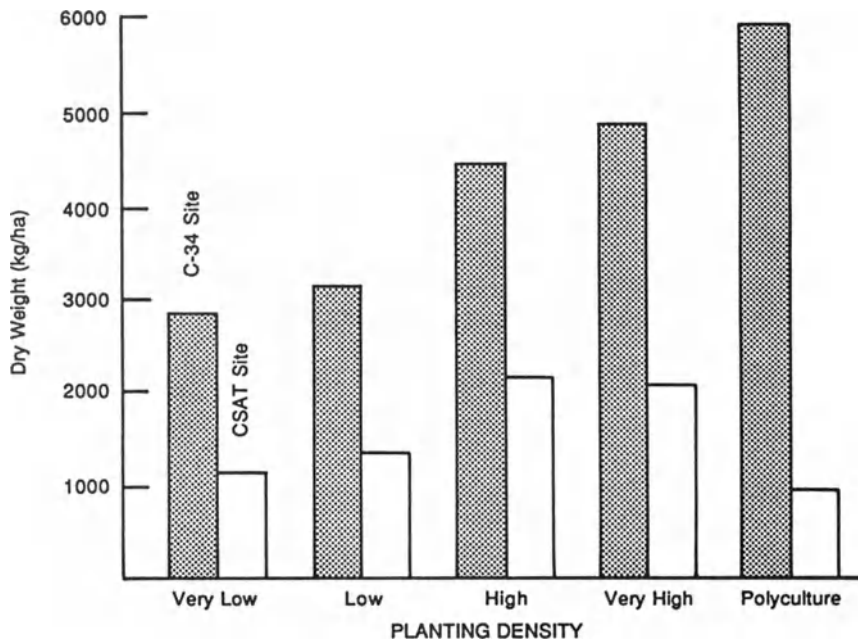


Figure 10.2. Biomass production by corn plants in polyculture, compared to four densities of planting in monoculture, at two sites in Cardenas, Tabasco, Mexico.

yield difference between weeded and unweeded plots was minimal for the high density—a very different trend from C-34.

Except for a small amount of fruit in the two low densities of weeded monoculture squash, no significant harvest was obtained. Excessive rainfall around the time of squash fruit development and harvest severely reduced the yield, an effect compounded by the slightly lower-lying, more compacted soil of the CSAT site.

Analysis of Variance of the results showed no significant differences due to density because of the great variability of yields between plots, but the effects of weeding did prove to be highly significant.

Biomass production followed the same tendencies observed for grain and fruit yields. Only the weeded plots are discussed here. For the C-34 site, corn plant biomass increased with the increase in monoculture density, but even so, the highest biomass production was achieved by plants in the polyculture (Figure 10.2). Biomass for corn plants in the CSAT site were much less than the C-34 site in all densities. The polyculture produced the lowest yield, and the highest yield was from the high-density monoculture planting. On the other hand, biomass production was comparatively higher for beans at the CSAT site than at the C-34 site (Figure 10.3). In both sites, the yields were highest at the highest densities and

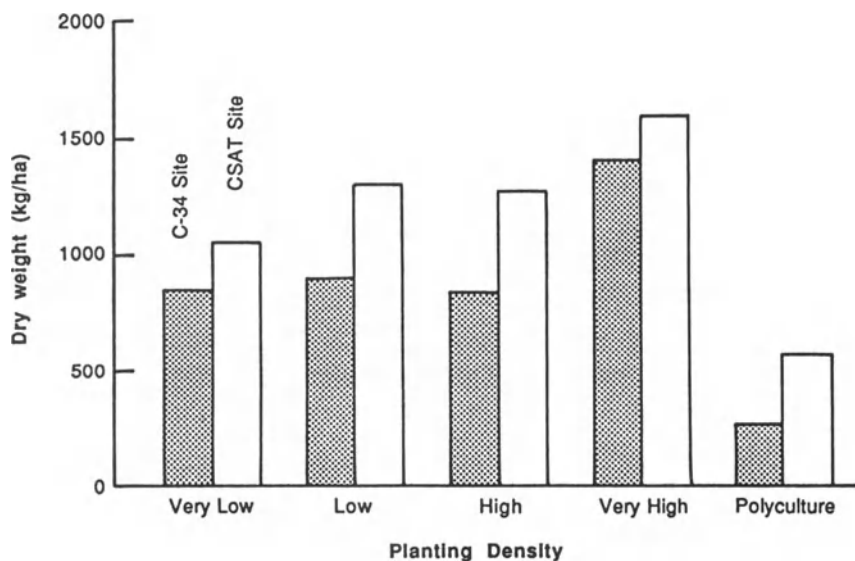


Figure 10.3. Biomass production by bean plants in polyculture, compared to four densities of planting in monoculture, at two sites in Cardenas, Tabasco, Mexico.

lowest in the polyculture planting. Squash data were available only from the C-34 site (Figure 10.4). The highest yield was obtained with the high-density planting. Interestingly, the lowest production of biomass was achieved with the very low monoculture density, and not with the polyculture.

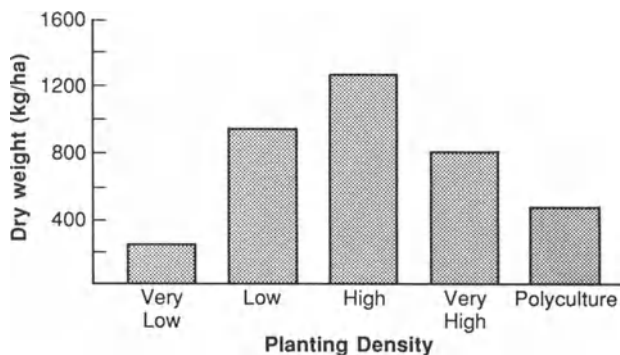


Figure 10.4. Biomass production by squash plants in polyculture, compared to four densities of planting in monoculture, at one site in Cardenas, Tabasco, Mexico.

Table 10.3. Land Use Equivalent ratios (LER's) for the corn, bean, and squash polyculture

LER	Normal Density	Highest Yield Density
Site C-34		
Yield	2.03	1.71
Biomass	1.18	0.89
Site CSAT		
Yield	0.91	0.56
Biomass	0.52	0.39

As can be seen in Table 10.3, overyielding occurred in only the C-34 site, where the land use equivalent ratios (LER) were greater than 1.0 for agricultural yields, comparing equivalent monoculture and polyculture yields, or when comparing the highest-yielding monoculture with the polyculture, independent of density. This implies that for this site, the polyculture system produced almost twice as much on the same area of cultivated land as the monocultures planted separately, with their yields summed. Biomass production overyielded only when the normal monoculture densities were compared to the polyculture. In all other cases, the mixture underyielded when compared to the sum of an equivalent area planted to each of the sole crops, implying no advantage to the crop mixture. Overyielding at one site and not at another demonstrates the importance of understanding how environmental conditions can effect the LER's, not just what crop mixture is used. The soils at the CSAT site have been worked with machinery and received frequent application of agrochemicals for at least the past 20 years, whereas the C-34 site has only been planted with traditional, low-input technologies using hand tools and occasional short fallows. The relationship between the management practices used at the two sites and overyielding in the crop mixtures is an exciting area for future research.

From this study it can be concluded that crop mixtures sometimes can overyield when compared to plantings of monocultures of the component crop species, but that such overyielding is affected greatly by different environmental factors. The response of corn, beans, and squash to increasing monoculture densities did not always show a typical yield/density curve as might have been expected, but the results obtained demonstrate the need to take into account the "equivalency" of monoculture densities when overyielding studies are being done. Weeding definitely improves yields, but doesn't always affect the LER's. Biomass seems to be a poorer indicator of overyielding ability of these crops, but further study is necessary to understand this phenomenon.

10.4 The Mechanisms of Overyielding

Once yield advantage has been demonstrated, studies that provide an understanding of the ecological mechanisms of the yield increase can then be carried out. Various studies have been done on the corn/bean/squash intercrop with this goal in mind. On the one hand, it appears that beans in polyculture with corn nodulate more and are potentially more active in biologically fixing nitrogen, which could be made directly available to the corn (Boucher, 1979). Net gains of nitrogen have been observed when the crops are associated, despite the removal of this nutrient with the harvest (Gliessman, 1982). This contributes to both the long term reduction in dependence on external purchased inputs of fertilizer, as well as an overall more stable basis for managing resources within the system.

At the same time, study of the management practices employed in this polyculture have demonstrated the ecological basis upon which the practices can function. For example, despite the lower squash yields in the mixed planting, farmers insist that the crop system benefits from the squash presence through the control of weeds (Gliessman, 1983). Thick, broad, horizontal leaves cast a dense shade that blocks sunlight, and leachates in rains washing the leaves contain allelopathic compounds that potentially inhibit weed growth. Herbivorous insects are at a disadvantage in the intercrop system (Risch, 1980; Altieri and Liebmann, 1986), and the presence of beneficial insects is promoted (Letourneau, 1983). Leaving weeds in the intercropped system can be advantageous as well (Chacon and Gliessman, 1982). *Chenopodium ambrosioides*, for example, has the potential for inhibiting plant pathogenic nematodes through the release of toxic root exudates (Garcia, 1979). *Lagascea mollis* can allelopathically control the invasion of weeds detrimental to the crops if it is allowed to form a dense cover after the critical establishment stage in crop development (the first 3 to 4 weeks), thus avoiding inhibition of the crop as well (Gliessman, 1983).

Understanding the dynamics of resource use and distribution in a mixed-crop system is very important as well. In a planting in Costa Rica, weed biomass was determined and compared in mature monocultures of corn, beans, and squash, and in the polyculture of all three (Bergmark et al., 1986). Plots were set up to test the hypothesis that the vegetative canopy of a polyculture system has a more complex structural diversity, hence an enhanced ability to capture incoming solar radiation. As a result, it was hypothesized that the increased shading possible in the polyculture should lead to a reduction in weed biomass. The plots were planted in May, followed by a uniform weeding 6 weeks later, and the final sampling of aboveground live biomass of the weeds was taken 5 weeks after that.

As can be seen in Table 10.4, there definitely are trends in weed-weight distribution according to the crop type, although variability in sample

Table 10.4. Mean fresh weight of above-ground weed biomass in corn, bean, and squash monocultures, compared to a polyculture of all three

Crop System	Mean Fresh Weight of Weeds ^a (gm/0.2 m ²)		% Light Transmission ^b
	Total	Monocots	
Maize monoculture	61.8	16.8	36.06 ± 03.8
Squash monoculture	61.4	20.8	51.40 ± 31.2
Bean monoculture	79.8	14.9	74.50 ± 22.7
Polyculture	55.0	19.0	44.70 ± 25.5

Source: Adapted from Bergmark et al., 1986.

^a Weed-weight values are the means of three samples taken in each plot.

^b Percentage of light transmission was determined by measurements at the soil surface in each crop system with a LI-COR quantum radiometer and PAR sensors. Light transmission values are the means of 10 readings taken at 50 cm intervals in each plot.

weights led to a lack of statistical significance between treatments. At the time of the sampling, the squash monoculture cover had only partially covered the plots, bean cover was fairly limited, and densest cover was observed in the corn monoculture and the polyculture. Total weed biomass under the corn and squash systems were the same. Total biomass from the bean plots was 23% greater and weed biomass from the polyculture system was approximately 10% less than the corn or squash systems. Monocots accounted for a lower proportion of the bean plot weed weight (about 10% of the total biomass) than they did in the corn (27% monocots), squash (34% monocots), or polyculture (35% monocots) plots. However, actual mean weights of the monocot biomass varied little between treatments. The percentage of light transmission (calculated as the percentage of transmitted light reaching the soil surface in each crop system, compared to that reaching an unplanted soil surface adjacent to the plots) showed similar trends, but high variability in this sampling again ruled out statistical significance. The highest light transmission was recorded in the bean monoculture, correlating with the lower cover produced by the bean crop. The lowest transmission occurred in the corn monoculture. The trend for lower weed biomass in the polyculture, then, is only partially related to light reception by the crop canopy. Many other factors are coming into play in such an interactive system, and detailed and long-term research is necessary to determine their relative importance (Gliessman, 1986).

10.5 Future Research Directions

Intercrop systems are agroecosystems with varying degrees of complexity in the mixed-species assemblages that farmers have selected over time

for different advantages that are perceived with the mixtures. Our understanding of the ecological basis of plant interactions in general has increased greatly (Harper, 1977; Gliessman 1986), providing the tools needed to better understand the manner in which individual plants in crop mixtures interact with their neighbors and utilize the resources that eventually are converted to harvestable biomass. Establishing optimal densities for highest yields in monoculture systems has come to depend on the massive alteration of the crop environment with large amounts of external energy and material sources that most often rely on a fossil-fuel base. Very little work has been done on the optimization of intercrop densities. Results presented in this chapter demonstrate the potential advantage that an intercrop system can provide to the farmer, but they also point out how important an understanding of the complex ecological interactions taking place in the mixture will be for agroecologists to reach the point where they will be able to confidently predict the outcome of any particular mixed crop arrangement. Complementarity of resource use must be found, beneficial modifications of the crop environment resulting from a mixture must be taken advantage of, and more efficient internalization of material flow must come about. A theoretical basis for evaluating intercrop systems is being developed (Vandermeer, 1984). Expanding the view of intercrop agroecosystems, then, must include such aspects as pest management, soil conservation, and optimal resource use on the one hand, and overyielding, crop diversification, and multiple-use benefits on the other. Together they will contribute to the development of a more resource-conserving and sustainable agriculture.

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11. Integrating Trees into Agriculture: The Home Garden Agroecosystem as an Example of Agroforestry in the Tropics

Stephen R. Gliessman

11.1 Introduction

The diversification of agroecosystems with the incorporation of trees is a practice that has a lengthy history. This is especially true in the tropical and subtropical regions of the world where farmers have long planted trees with other agricultural crops and incorporated animals to help provide for the basic needs of food, wood products, and fodder, and to help conserve and protect their often limited resources (Nair, 1983). In the past decade, particular interest has developed in the many variations of this practice, and with it, an awareness of the unique productive and protective value of trees in agricultural systems (Felker and Bandurski, 1979; McDaniels and Lieberman, 1979; Getahun et al., 1982; Nair, 1983; Organization for Tropical Studies (OTS), 1986).

The term *agroforestry* has been given to practices that deliberately or intentionally mix or retain trees in the crop/animal production fields (Wiersum, 1981; Nair, 1983). It combines elements of agriculture, whether crops or animals, with elements of forestry in production systems on the same piece of land, either simultaneously or sequentially. Because present-day concepts of agroforestry are just now being developed, there is no single definition for it (Chandler and Spurgeon, 1980). The variety of definitions may in fact reflect the great variations in the practice, according to Budowski (1983).

11.2 Research on Integrated Agroecosystems

The objective of most agroforestry systems is to optimize the beneficial effects of interactions of the woody components with the crop or animal components to obtain more diversity of products, to lessen the need for outside inputs for the management of the systems, and to lower the environmental impacts of farming practices (Gliessman et al., 1981; Gliessman, 1984). Systems that show a range of complexities result and many of the same techniques used to study multiple cropping systems can be used for the study of these agroforestry systems. Thus agrosilviculture (the management of agroecosystems combining agricultural crops and trees) and even silvopastoral systems (animal production systems that incorporate trees) are similar to the inter- and mixed-cropped types of multiple cropping.

A major step in the study of any complex agroecosystem, and especially agroforestry systems, is to determine the patterns of species distribution, dominance, and diversity. An understanding of community structure leads to better knowledge about either actual or potential resource use by that system, the dynamics of species interactions as affected by the trees, and the impacts of the trees on biotic and abiotic factors (Huxley, 1985). Only after gaining an understanding of the organization of the agroecosystem can we begin to focus on the complex ecological processes that determine both productivity and sustainability. This understanding can then be linked to the intricate social and economic factors that currently have greatest input in determining how an agroecosystem is designed and managed. In agroforestry systems, trees can fill both ecological and cultural roles.

11.3 Tropical Home Gardens

The agroforestry system that shows the greatest complexity and diversity is the tropical home garden system. Probably one of the most complex and interesting agroecosystems, and possibly the one we have most to learn from regarding resource management for a sustainable agriculture, home gardens are found in a concentrated area around the dwelling of most farming systems throughout the tropics and subtropics. The home garden is an integrated ecosystem of humans, plants, animals, soils, and water, with trees playing key roles in both the ecology and management of the system. Variouslly defined as kitchen, orchard, mixed, or forest gardens, the term home garden appears to be the most broadly used terminology for describing a piece of land with definite boundaries, usually near a house, occupying an area generally between 0.5 and 2.0 ha. (Allison, 1983; Budowski, 1985; Ninez, 1985). They are rich in plant species, usually dominated by woody perennials, and are generally de-

Table 11.1 Characteristics of home garden agroforestry systems at upland (Tepeyanco, Tlaxcala) and lowland (Cupilco, Tabasco) sites in Mexico^a

Characteristic	Cupilco	Tepeyanco
Average garden size (ha)	0.70	0.34
No. of useful species per garden	55.00	33.00
Diversity (bits)	3.84	2.43
Leaf area index ^b	4.50	3.20
% Cover	96.70	85.30
% Light transmission	21.50	30.50
Perennial species (%)	52.30	24.50
Tree species (%)	30.70	12.30
Ornamental plants (%)	7.00	9.00
Medicinal plants (%)	2.00	2.80

Source: After Allison, 1983.

^a Data from 4 gardens in Tepeyanco and 3 gardens in Cupilco.

^b Calculated using a drop line interception method.

scribed as being stratified or multistoried (Christanty, 1981; Alcorn, 1984). A mixture of annuals and perennials of different heights forms layers of vegetation resembling a natural forest structure. The high diversity of species permits year-round harvesting of food products, as well as a wide range of other products used by the inhabitants, such as fire wood, medicinal plants, spices, and ornamentals (Gonzalez, 1985; Christanty et al., 1986).

In a study of home gardens in both upland and lowland sites in Mexico, it was found that in quite small areas (between 0.3 and 0.7 ha), high diversity permitted the maintenance of gardens that in some aspects were similar to the local natural ecosystems (Allison, 1983). For example, the gardens studied had relatively high indices of diversity for cropping systems (Table 11.1), and had leaf area indices and cover levels that approximated the much more complex natural ecosystems of the surrounding regions. In a study by Ewel et al. (1982), in which nine different tropical ecosystems were analyzed for a series of ecosystem characteristics, a 40-year-old home garden had the most evenly distributed canopy that was fairly uniformly stratified from ground level to over 14 m in height. Its leaf area index was 3.9, percentage of cover was 100%, and the leaf biomass/m² was the next to highest for all of the ecosystems examined (307 g/m²). Total root biomass/m² to a depth of 25 cm was identical to leaf biomass (307.2 g/m²). Most importantly, of the nine systems tested, the home garden had the highest root surface area of small diameter roots (< 5cm) with a value of 2.1 m²/m² of ground surface to a depth of 25 cm. These traits are indicative of an ecologically more efficient system, especially in its ability to capture light, garner nutrients in the upper layers of the soil, and store nutrients in the aboveground biomass, at the same time reducing the impact of rain and sun on the

Table 11.2. Comparison of plant species in a home garden over 2 years in Cañas, Guanacaste, Costa Rica^a

	1985	1986
Number of species	71	83
Number of individuals	940	1870
Number of tree species	17	16
Number of food species	21	18
Number of ornamental species	23	31
Number of medicinal species	7	9
Number of firewood species	3	5
Number of spice species	0	4

^a Garden size is 1240 m².

soil. Space between layers may increase carbon dioxide availability for photosynthesis. Layers themselves may increase habitat diversity for birds and insects and may be useful for maintaining better biological control in the system (Altieri, 1986). Nutrients can be efficiently recycled through both ecological diversity and human manipulation (Soemarwoto and Soemarwoto, 1979).

An important aspect common to home gardens is the multiple uses that the various garden elements have (Table 11.2). A cash crop, such as coconut, can also serve as a subsistence food. Some parts are used as fuel, others for construction. Different plants or animals serve as important sources of carbohydrates, protein, vitamins, and minerals (Dewey, 1979). For example, the fruit of the mango tree provides an excellent source of Vitamins C and A. Because of the mixture of species, there is always something ready to be harvested, adding diversity to the diet. Many products can be sold for cash or traded. Variability in flowering and maturity ensures harvest, or even sale for income during the entire year (Gliessman et al., 1981).

The functions of the home garden can include such social or aesthetic functions as serving as an indication of the social status of the owner, or beautifying or improving the environment directly associated with the house. At the same time, the gardens can provide an important role in the economy of rural families. Generally, the more isolated the dwelling, the greater emphasis on subsistence crops. In studies in Java (Hisyam et al., 1979), it was found that production in local gardens fell considerably during the rice harvest when labor was concentrated on that cash crop, but during the rest of the year, activity in the gardens was quite high. Between 20 and 30% of the annual income of many households was obtained from their home gardens.

The few studies on home gardens that have followed them over time have shown that the gardens are dynamic and changing. In a study carried out by students of the Organization for Tropical Studies Agroecology



Figure 11.1. A complex home garden agroecosystem near Puerto Viejo, Sarapiquí, Costa Rica. Photo by S. Gliessman.

Course (OTS 85-4) in Costa Rica, a home garden near Puerto Viejo (Figure 11.1) was shown to be in the process of change due to a need for cash income, as well as the limited availability of both land and labor (Flietner, 1985). The tree stratum in approximately one-half of the 3264 m² garden was in the process of being replaced with coconuts planted in evenly spaced rows, and the understory had been planted to pure stands of yuca (*Manihot esculenta*) and pineapple (*Ananas comosus*). With the construction of an all-weather road to the region, trucks are more available for hauling produce to distant urban markets, creating a demand that a few years before did not exist. Farmers are adjusting their agroecosystems to meet this demand. Also, because the farmer has recently taken a job off the farm, he is less available to meet the management needs that a more diverse home garden requires. As the coconuts mature and generate a much shadier environment on the ground below them, the farmer will have to decide what shifts will be necessary in the understory plants. He may shift to the malanga (*Colocasia esculenta*), common already in the shadier parts of the garden. Over time, though, there are advantages to diversifying production to include crops for both market and home use.

In a long-term study of traditional agriculture in Tlaxcala, Mexico, Gonzalez (1985) has been able to document the changes that have taken

place in home garden diversity, structure, and management, because this state in the upland, central region of Mexico has gone through industrialization and population increase. The number of species is often reduced, more orderly, easily managed cropping patterns are used, and species are planted that more easily enter the cash economy. Interestingly, though, Tlaxcala has gone through several "boom and bust" cycles where off-farm employment has been alternately available and then limited. The rise and fall of flour mills in the nineteenth century, or the *bracero* program in the U.S. during the 1950s, are examples of work or markets being available then closing down. This ebb and flow has generated a certain mistrust of job security off the farm. As a result, more diverse agroecosystems are maintained even in times of off-farm employment as insurance against the probable loss of the outside income. This is reflected especially in the diverse home-garden systems (Allison, 1983; Gonzalez, 1985).

Gonzalez has also been able to document how population growth can impact garden structure. Because Tlaxcala is close to the large and expanding urban-industrial centers of Puebla and Mexico City, there is considerable demand and market for a large variety of agricultural products, from basic corn and beans, to vegetables and cut flowers. This is a stimulus to diversify the cropping systems, but it is also a stimulus to put greater emphasis on cash crops and abandon many subsistence species. It is those families that see the advantage to combining both cash and subsistence crops who maintain the most diverse home gardens. And they often do this because of perceived advantages that are gained from the crop mixtures, advantages that can come about through the ecological impact of the trees on the overall system. In a home-garden system studied in Cañas, Guanacaste, Costa Rica, interesting shifts in diversity and organization of the garden were observed to take place from one year to the next (Gliessman, unpublished). As can be seen in Table 11.2, there were interesting changes in species composition from June 1985 to June 1986. The total number of species in the garden increased by 12, but more impressive is the major increase in total number of individual plants. A large part of this increase came primarily from the greater predominance of ornamental species the second year. Some of the food species that had been very common the year before, such as squash, were not present in 1986 due to a drought that had eliminated seedlings planted earlier. In fact, the woman of the household, who actually did most of the work required to maintain the garden because her husband had a job in the nearby town, mentioned that the dry year had made it difficult to maintain the garden because they had no source of irrigation other than water that would have to be hauled by hand from a nearby river. She also stated that she had less time to care for the garden because she and her daughters had recently begun a small-scale bread-baking business for marketing in the local community. Some space in the garden (only 1240

m²) was being taken up by stored firewood for baking. Ornamental, medicinal, and spice plants were much more common, and thrived in diverse mixtures around the well, outdoor shower, and wash basin, where water was either intentionally or accidentally provided for them. Undoubtedly, with time the garden will change more. It is probable that if the baking business fails, the emphasis on food crops will once again be greater. It is important to be aware that part of the change is for ecological reasons, and part is more socioeconomic in nature. This change can be quite rapid.

11.4 Future Directions

The ability of an agroecosystem to respond to different factors or conditions in the environment, to meet the needs of the inhabitants for a great diversity of products and materials, and to respond to external socioeconomic demands are all very important components of a sustainable system. At the same time, we have become more aware of the need to find ways to lessen dependence on expensive, imported agricultural inputs, as well as to limit the environmental impacts of the ways we farm. What we are learning from agroforestry systems, such as home gardens, is that there are practical, time-tested ways to combine all of these characteristics into manageable, productive, and sustainable farm units. Trees are the key elements in the functioning of the system.

More information on the already-existing types of home garden agroecosystems is desperately needed. The rapid move towards urbanization and cash cropping in developing countries is threatening the existence of such local systems. The information presented at the First International Workshop on Tropical Homegardens held in Indonesia in 1985 was a major step forward, and fortunately more such workshops are planned for the near future. The next step is to set up and monitor model home gardens that incorporate traditional knowledge with selected modern, agricultural improvements. Two such systems that have attempted such modeling are known from lowland Mexico (Chavelas, 1979; Gliessman et al., 1981), but they have suffered from a lack of institutional support that seems to come from a general lack of appreciation in the agricultural research establishment for the potential value of such systems.

The more widespread implementation and improvement of agroforestry systems will involve considerable research on the part of agroecologists and social scientists. By applying interdisciplinary research methods, improvement can take place towards reestablishing the much-needed ecological balance that underlies a sustainable agriculture, as well as accommodating the complex socioeconomic interactions that revolve around such systems. Most importantly, much of the basic knowledge of such systems still lies with the traditional farmer.

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12. The Influence of Trees in Selected Agroecosystems in Mexico

John Farrell

12.1 Introduction

The careful integration of trees with other agricultural activities is thought to enhance the long-term sustainability and productivity of many agroecosystems. This is generally attributed to the role these trees play in controlling erosion, maintaining soil organic matter, improving nutrient cycling efficiency, and ameliorating microclimates (Steppler and Nair, 1987).

To help illustrate the degree of influence trees may have on certain agroecosystem properties, I will summarize selected results from a study conducted in Tlaxcala, Mexico. The objective of this study was to determine to what degree trees modify the growing environment of under-story crops and whether these changes affect crop growth and yields.

Traditional farming systems of Tlaxcala offer a unique opportunity to study the relationships between trees and other agroecosystem components. In the lower elevation plains, *Prunus capuli*, *Juniperus deppeana*, *Crataegus mexicana*, *Prunus persica*, and *Buddleja americana* are commonly maintained along field borders or left scattered within fields, often with crops planted right up to their base. Higher tree densities can be found where narrow fields have been cleared within dense woodlands and planted to crops. In wetter areas, trees and crops are also mixed in orchards, where apple, peach, plum, and pear-apple may be found interplanted with maize, barley, wheat, alfalfa, *Agave* spp., and *Opuntia* spp.

Two of the most common trees found growing in association with agricultural crops, *Prunus capuli* and *Juniperus deppeana*, were chosen for determining the influence of individual isolated trees on surface soil properties, soil moisture, soil and air temperatures, relative humidity, and growth and yield of associated maize plants. In addition, measurements of soil properties and crop yields were taken in a maize field bordered by a stand of *Alnus firmifolia* to determine the degree of influence of these shelterbelt trees.

12.2 Methods

Five suitable *Prunus* and *Juniperus* trees growing in cultivated maize fields were selected for sampling. Of these five trees, two were randomly chosen for sampling surface-soil chemical properties. The two *Prunus* were located on Eutric Regosol soil and the *Juniperus* were found on Eutric Fluvisol. Soil samples were collected to a depth of 15 cm at distances of 2, 6, 10, 14, 18, and 22 m from the base of the trees, along four randomly placed transects. At each location two subsamples were collected and mixed for analysis according to the procedures described by Black et al. (1965). A number of soil properties were measured: total nitrogen (by macro-kjeldahl), water soluble phosphorus (determined colorimetrically), total carbon (by dry combustion), pH (with a glass electrode using a water-saturated soil paste), and cation exchange capacity. Exchangeable potassium, calcium, and magnesium were displaced with a 1N ammonium acetate solution buffered to pH 7 and determined by atomic absorption spectrophotometry. Water-holding capacity was determined gravimetrically on samples brought to equilibrium on a semi-permeable ceramic plate maintained at a pressure differential of $\frac{1}{3}$ and 15 bars.

Three *Prunus* and *Juniperus* trees were randomly selected for soil moisture sampling. Five zones were identified to represent various areas of tree influence, within which sampling was carried out. These zones included the canopy zone, west shade zone, east shade zone, root zone, and zone of no tree influence (Figure 12.1). Five soil samples were taken from 0 to 15 cm and 15 to 30 cm depths in each of the designated zones. Three random subsamples were collected per sample, mixed, and soil moisture was measured gravimetrically. Sampling was conducted three times during the crop season; twice during early maize development, while plant growth was uniform in all five zones; and once after maize had matured, and water uptake had ceased.

Surface soil temperatures (1 cm) were measured around four *Prunus* and *Juniperus* trees at three random points midway between the tree stem and canopy line and 20 m from the tree in the open. Readings were taken at midday on five different occasions while the maize was growing,

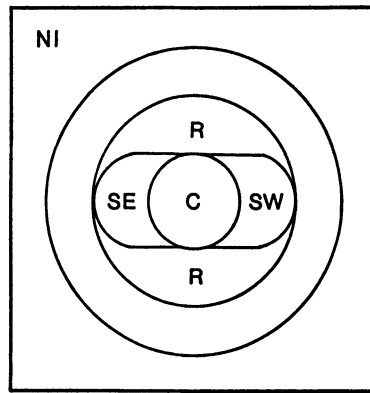


Figure 12.1. A diagrammatic representation of sampling zones around individual trees in Tlaxcala, Mexico. C = canopy; SE = shade (east); SW = shade (west); R = root; and NI = no influence.

and again after the maize had been harvested. Midday air temperature was measured at a height of 1.5 m at the same time and location as soil temperature. Measurements of minimum air temperatures were taken under the canopy and 25 m from a single *Prunus* tree located in the center of a cleanly cultivated field. Minimum/maximum thermometers were placed 1.5 m above the ground throughout the night, six times during November. Relative humidity was measured with a wet/dry bulb sling psychrometer at the same time and location as midday air temperatures.

Height and grain yield of maize plants cultivated around four *Prunus* and *Juniperus* trees were measured after the maize had fully matured. Height measurements were taken of fifteen randomly selected plants in the canopy and shade zones and twenty plants in the root and no-influence zones. An indirect measurement of grain yield was used by determining the length and basal diameter of each ear along three, four and five 4-m transects randomly placed along rows within the canopy and shade zones, root zone, and no-influence zone, respectively. A yield index was then obtained by multiplying length by diameter of each ear.

To measure the degree of influence that stands of trees have along cultivated field borders, an area was chosen where a woodland of natural vegetation (dominated by *Alnus firmifolia* trees) had been cleared for cultivation, leaving a patchwork of cropped fields interwoven with wide rows of trees. A 25-meter by 90-meter maize field within this woodland was selected for measuring maize yield and soil properties. The field was bordered on one side by a 15-meter wide stand of *Alnus* and on the other by another maize field.

To compare potential differences as a function of distance from the trees, sampling was carried out along the first, center and outside rows

of the field, or 1 m, 13 m, and 26 m, respectively, from the tree border. Height of twenty random maize plants was measured in each of the three rows, and yield measurements were taken along four random 4-meter transects. Soil moisture samples (0 to 15 and 15 to 30 cm) were also collected from the three rows. Three random subsamples per five samples were mixed, and soil moisture was determined gravimetrically. Surface soil samples (0 to 15 cm) were collected in the same manner for analysis of chemical and physical properties. Samples were analyzed using the methods described above.

12.3 Results and Discussion

12.3.1 Individual Tree Influences

12.3.1.1 Soil Chemical Properties

The degree to which trees influence surface soil properties depends on the species of tree and the property measured (Table 12.1). For *Prunus* and *Juniperus* trees, higher values of all properties were found beneath the tree canopies, and a decreasing gradient was observed with increasing distance from the trees. Differences between soil properties beneath the canopies and in the open were especially pronounced for available phosphorus, total carbon and nitrogen, and exchangeable potassium and magnesium. The sphere of influence of both trees appears to extend 6 to 10 m from their trunk.

Soil enrichment has also been reported beneath *Acacia albida* in the African Sahel (Charreu and Vidal, 1967; Dancette and Poulain, 1969; Felker, 1982), beneath *Prosopis juliflora* in arid rangelands of southwestern United States (Tiedemann and Klemmedson, 1977), and near *Erythrina glauca* shade trees in Brazilian cacao plantations (Cadima and Alvim, 1967). These three leguminous trees reportedly have a marked effect on increasing soil nitrogen, total carbon, and exchangeable cations (Table 12.2). Higher concentrations were found beneath all the trees, although the degree of differences varied depending on the particular trees studied. *Prosopis* had no effect on potassium levels, and though a trend is indicated for amounts of phosphorus at different locations, these values are not significantly different ($p = .05$). No explanation was given for the greater amounts of phosphorus found in the open compared to beneath *Erythrina* trees. Unlike *Prunus* and *Juniperus*, this species had no influence on surface soil pH.

Soil enrichment near trees has been attributed to their role in the efficient cycling of nutrients (Zinke, 1962; Bernhart and Poupon, 1980; Nair, 1984). Trees are capable of translocating nutrients from soil depths inaccessible to most annual crops, and through litterfall and decaying

Table 12.1. Surface soil properties at six distances from the base of individual *Prunus capuli* and *Juniperus deppeana* trees^a

Distance (m)	pH	C (%)	N (%)	P ₂ O ₅ (ppm)	CEC (meq/100 g)	Exchangeable			Water-holding Capacity	
						Ca (meq/100 g)	Mg (meq/100 g)	K	1/3 bar (%)	15 bar (%)
<i>Prunus</i>										
2	6.6 ± .26	1.34 ± .04	.091 ± .001	17.3 ± 0.58	7.0 ± 0.48	6.5 ± .05	1.29 ± .23	.58 ± .04	11.1 ± 1.00	5.9 ± .22
6	6.4 ± .28	.73 ± .23	.051 ± .012	6.6 ± 2.19	5.2 ± 1.26	3.9 ± .69	.69 ± .08	.26 ± .00	10.4 ± 1.30	4.4 ± .21
10	6.2 ± .18	.60 ± .20	.041 ± .009	3.4 ± 0.97	4.8 ± 1.00	3.0 ± .35	.52 ± .11	.19 ± .01	9.6 ± 0.75	3.9 ± .11
14	6.0 ± .00	.47 ± .12	.031 ± .005	2.3 ± 1.01	4.1 ± 0.85	2.3 ± .20	.40 ± .09	.17 ± .02	8.8 ± 0.14	3.6 ± .12
18	5.8 ± .05	.43 ± .11	.028 ± .003	2.0 ± 1.00	4.1 ± 0.71	2.1 ± .32	.34 ± .09	.15 ± .01	8.1 ± 0.71	3.4 ± .12
22	5.9 ± .09	.50 ± .12	.033 ± .005	2.2 ± 0.87	4.6 ± 0.60	2.6 ± .64	.34 ± .08	.18 ± .03	8.8 ± 0.62	3.7 ± .00
<i>Juniperus</i>										
2	7.4 ± .01	.63 ± .10	.044 ± .008	2.5 ± 1.06	6.4 ± 0.69	6.6 ± .10	1.24 ± .15	.84 ± .13	9.2 ± 0.56	5.4 ± .52
6	6.9 ± .15	.51 ± .07	.038 ± .001	1.3 ± 0.18	6.0 ± 0.37	5.1 ± .49	.97 ± .01	.58 ± .03	8.4 ± 0.22	5.1 ± .25
10	6.5 ± .13	.36 ± .02	.030 ± .000	.6 ± 0.04	5.5 ± 0.69	4.1 ± .17	.85 ± .04	.48 ± .00	8.2 ± 0.14	5.0 ± .28
14	6.6 ± .05	.37 ± .06	.033 ± .001	1.4 ± 0.39	5.7 ± 0.03	4.2 ± .50	.97 ± .14	.47 ± .01	8.2 ± 0.08	5.2 ± .01
18	6.7 ± .38	.40 ± .01	.031 ± .001	2.2 ± 0.83	5.5 ± 0.08	4.5 ± .36	.98 ± .03	.56 ± .03	8.4 ± 0.39	5.1 ± .01
22	6.4 ± .21	.40 ± .02	.030 ± .001	1.5 ± 0.53	5.6 ± 0.27	4.3 ± .29	.89 ± .03	.48 ± .02	8.3 ± 0.18	5.1 ± .12

^a Mean values ± S.E.

Table 12.2. Surface soil nutrient concentrations beneath the canopy of selected trees and in the open

	pH	C (%)	N (%)	P ₂ O ₅ (ppm)	Exchangeable		
					Ca	Mg (meq/100 g)	K
<i>Acacia albida</i> ^a							
Canopy	6.4	5.3	0.60	35	29.4	11.2	1.00
Open	6.1	3.3	0.31	15	14.7	6.3	0.70
<i>Acacia albida</i> ^b							
Canopy	5.3	3.7	0.40	49	1.6	0.7	0.10
Open	5.1	2.7	0.30	37	1.1	0.6	0.07
<i>Prosopis juliflora</i> ^c							
Canopy	6.3	0.9	0.05	.03 ^e	—	—	2.95
Open	6.4	0.4	0.03	.03 ^e	—	—	2.98
<i>Erythrina glauca</i> ^d							
Canopy	4.8	1.3	0.15	3.6	4.0	2.2	0.28
Open	4.7	0.9	0.12	6.7	2.6	1.5	0.11

^a After Charreu and Vidal, 1967.^b After Dancette and Poulain, 1969.^c After Tiedemann and Klemmedson, 1977.^d After Cadima and Alvim, 1967.^e Percentage of P.

roots, these nutrients tend to accumulate in the surface soil layers near the trees. Throughfall and stem flow may also be important in nutrient cycling and may contribute significant amounts of mineral nutrients to the soil surface (Kellman, 1979; Parker, 1983). Dancette and Poulain (1969) calculated that on a per hectare basis, the *Acacia* trees they studied contributed 5.3 tons of dry organic matter and 300 kg of nitrogen to the soil beneath their canopies. They argued that to reproduce these levels outside the influence of the trees would require large quantities of mineral and organic fertilizers—far beyond the capabilities of the average farmer in Senegal. Felker (1978) proposed that the presence of *A. albida* on farms in the Sahelian zone could more than double land-carrying capacity and permit a more sedentary, permanent agriculture by eliminating the need for fallow periods.

12.3.1.2 Soil Moisture

Significant differences ($p = .05$) in surface soil moisture (0 to 15 cm) were found between zones around *Prunus* and *Juniperus* trees (Table 12.3). The soil was moistest beneath the tree canopies, somewhat drier in the shade zones, and driest in the root and no-influence zones. No differences were observed between the root and no-influence zones at the 0 to 15 cm depth nor between any of the zones at the 15 to 30 cm depth. Differences were most pronounced around *Prunus* trees.

Table 12.3. Surface soil moisture in five zones around *Prunus capuli* and *Juniperus deppeana* trees

Zone*	Soil Moisture (% dry wt. soil)	
	0 to 15 cm	15 to 30 cm
<i>Prunus</i>		
C	8.9 ± 0.9a**	8.9 ± 0.6a
SE	7.2 ± 0.5c	8.3 ± 0.4a
SW	8.1 ± 0.8b	8.6 ± 0.2a
R	7.1 ± 0.6c	8.1 ± 0.6a
NI	6.9 ± 0.7c	8.3 ± 0.3a
<i>Juniperus</i>		
C	7.4 ± 0.3a	8.1 ± 0.1a
SE	6.8 ± 0.4abc	9.4 ± 0.8a
SW	6.8 ± 0.3ab	8.7 ± 0.4a
R	6.4 ± 0.4bc	8.7 ± 0.5a
NI	6.1 ± 0.6c	8.6 ± 0.4a

* C = canopy, SE = shade-east, SW = shade-west, R = root, NI = no influence.

** Mean values ± SE; values compared across zones without one or more common letters are significantly different at the 5% level.

Although evaporation rates were not measured, these results indicate that shading by the tree canopies helps reduce surface soil moisture loss. Differences in evaporation between shaded and unshaded soil can be especially pronounced in Tlaxcala due to a high incidence of solar radiation, high temperatures, low humidity, moderate to strong winds, and sandy soils (Secretaría Programación y Presupuesto, SPP 1981). The increased capacity of soil under *Prunus* and *Juniperus* to retain water compared to soil in the open (Table 12.1), due to increased organic matter beneath the trees, also contributes to soil moisture differences in these zones. Although these two species have extensive and rather superficial root systems, a comparison of mean moisture levels in the root and no-influence zones (Table 12.3) suggests a minimal amount of water use in the upper 30 cm of soil.

Surface soil moisture (0 to 30 cm) near *Erythrina* trees were also found to be greater than at a distance from them during a 1-year period (Cadima and Alvim, 1967). However, the opposite was found to be true at depths of 30 to 60 cm and 60 to 90 cm, with soil moisture being greater at a distance from the trees. These observed differences in soil moisture were attributed to the distribution of *Erythrina* roots. In the upper 30 cm of soil, higher densities of fine roots were observed away from the trees than close to them, although at the two deeper depths, more fine roots were counted near the trees.

In comparing soil humidity profiles under and outside *Acacia albida*, Dancette and Poulain (1969) identified two zones differentially influenced by the trees. To a depth of 120 cm, they observed the stock of water to

increase 19% more beneath the trees than outside their canopy over the rainy season. They related this pattern to the reduction in evaporation under the trees. Between 120 and 400 cm, soil moisture increased 10% more away from the trees than beneath them. It was assumed that tree roots at this depth draw off more water beneath the *Acacia* than at a distance from them.

In addition to their influence on soil moisture through reducing evaporation, absorbing water, and increasing soil water retention, trees can influence the amount of water reaching the soil surface. Depending on the intensity of rainfall, tree canopies may either reduce or increase the water reaching the ground. Under conditions of heavy driving rains, over 20% more water was collected beneath *Acacia* trees than outside the trees (Dancette and Poulain, 1969). However, light rains resulted in a 4% reduction in rainfall beneath the *Acacia*. Similarly, the amount of rainfall collected beneath *Quercus rotundifolia* was either greater or less than that collected in the open, depending on the time of year (Calabuig et al., 1980).

Precipitation in the form of mist, fog, or cloud water can also be collected by tree canopies and may represent a source of large quantities of water beneath a tree (Vogelman et al., 1968; Azevedo and Morgan, 1974). Canopy drip from intercepted fog moisture by *Prunus* and *Juniperus* was often sufficient to entirely wet the soil surface beneath the tree canopies. The significance of this quantity of water is not known but does reduce the rate of soil drying.

12.3.1.3 Soil Temperature

Surface soil temperatures were between 13 and 15 degrees Centigrade lower beneath *Prunus* and *Juniperus* trees than in the open (Table 12.4). Differences tended to be slightly greater for *Prunus*. Interception of incoming radiation by tree canopies will cause such temperature differences because radiation is the primary source of soil heat. The sandy, organic-matter-poor nature of these soils, having a propensity for heating rapidly, helps magnify differences between locations.

12.3.1.4 Air Temperature and Relative Humidity

The canopies of both *Prunus* and *Juniperus* were found to have a slightly moderating influence on fluctuations of air temperature, although they had no significant influence on relative humidity at the height measured (Tables 12.4 and 12.5). Differences in relative humidity recorded when maize was present were most likely due to the difference in evapotranspiration between shaded and unshaded maize plants.

The buffering effect that trees have on air temperature fluctuations within forests and the general increase of relative humidity within forest stands is well recognized (Kittredge, 1948; Seitz, 1976). However, the

Table 12.4. Midday air temperature, relative humidity, and soil temperature at 1 cm depth beneath *Prunus* and *Juniperus* canopies and in the open; with and without maize present

	Air Temperature (°C)		Relative Humidity		Soil Temperature (°C)	
	With	Without	With	Without	With	Without
<i>Prunus</i>						
Canopy	21.0 ± 0.2a*	21.2 ± 0.4a	48.0 ± 1.7a	40.3 ± 2.1a	18.7 ± 0.4a	23.2 ± 0.6a
Open	23.1 ± 0.2b	22.3 ± 0.3a	51.9 ± 1.9b	40.0 ± 2.1a	34.2 ± 1.3b	37.6 ± 1.0b
<i>Juniperus</i>						
Canopy	22.2 ± 0.2a	20.9 ± 0.5a	47.4 ± 1.5a	42.6 ± 2.1a	22.5 ± 0.7a	22.2 ± 0.8a
Open	23.5 ± 0.2b	22.2 ± 0.5b	50.5 ± 1.7a	42.3 ± 2.4a	36.8 ± 1.1b	35.5 ± 0.9b

* Mean values ± SE; values compared across locations without one or more common letters are significantly different at the 5% level.

Table 12.5. Minimum temperatures measured beneath the canopy of a single *Prunus capuli* tree and in the open during November, 1983

Date	Temperature (°C)	
	Canopy	Open
11/04	-1.2	-1.8
11/05	2.0	1.3
11/12	1.0	0.4
11/16	0.0	-0.7
11/17	0.5	-0.1
11/28	6.5	5.8

relatively small degree of influence of individual *Prunus* and *Juniperus* trees is neutralized by prevailing winds that transfer both heat and moisture.

12.3.1.5 Maize Yields

A 50% reduction in maize grain yield was found beneath *Prunus* and *Juniperus* canopies compared to outside, but no significant differences ($p = .05$) were observed between the other four zones (Table 12.6). Height of maize plants was 10% less under *Prunus* and 20% less under *Juniperus* compared to the other zones. Light appears to be the limiting factor beneath the tree canopies, and any benefits from improved soil fertility and moisture near the trees are outweighed by the reduced light. In a study of the influence of *Tectona grandis* on intercropped maize, canopy light interception was also determined to be the primary cause for the reduction of maize yield under the trees (Verinumbe and Okali, 1985). Water and nutrient uptake by the *Prunus* and *Juniperus* trees had no detrimental effect on maize yields, as indicated by yield comparisons between root and no-influence zones.

Table 12.6. Yield and height of maize growing in five zones around individual *Prunus* and *Juniperus* trees

Zone*	<i>Prunus</i>		<i>Juniperus</i>	
	Yield**	Height (cm)	Yield	Height (cm)
C	452 ± 54b***	169 ± 3b	542 ± 71b	149 ± 5b
SE	999 ± 115a	191 ± 3a	1007 ± 69a	186 ± 3a
SW	993 ± 165a	188 ± 3a	900 ± 65a	183 ± 4a
R	1066 ± 164a	189 ± 2a	1047 ± 91a	182 ± 3a
NI	1005 ± 99a	192 ± 3a	1073 ± 52a	191 ± 3a

* C = canopy, SE = shade-east, SW = shade-west, R = root, NI = no influence.

** Yield expressed as a relative index per 4-m transect.

*** Mean values ± SE. Values compared among zones without one or more common letters are significantly different at the 5% level.

In comparison, Poschen (1986) found maize yields in Ethiopia were up to 75% higher and sorghum yields over 50% higher beneath *Acacia albida* canopies than in the open. These yield increases are consistent with those reported for sorghum, millet, and groundnuts beneath *A. albida* in other studies as well (Charreu and Vidal, 1967; Dancette and Poulain, 1969; Felker, 1978). Higher crop yields beneath the trees have been attributed to the improved soil fertility and water holding capacity near *Acacia*. Differences in soil microbiological characteristics beneath the trees and away from them may also help explain crop yield differences. Jung (1967) found increases in invertase, dehydrogenase, asparaginase, and respiratory CO₂ under the trees. There was also a marked increase in fungi and actinomycetes populations. Thus, organic matter decomposition and release of plant nutrients may proceed at a faster rate in soil beneath *A. albida*. An important characteristic of *A. albida* that makes it such a suitable overstory tree is its habit of being leafless during the understory crop's growing season. Thus there is little light interception by the tree canopy to inhibit crop growth.

12.3.2 Shelterbelt Trees, Soil Properties, and Maize Yield

The stand of *Alnus firmifolia* bordering the sampled maize field had an enriching effect on soil properties in that field, with the degree of influence being correlated with distance from the trees (Table 12.7). For all but pH and P, soil nutrient concentrations were highest along the field border nearest the trees and decreased with increasing distance from the trees. Differences between the nearest and farthest row were especially large for C, N, Ca, and Mg; levels were up to two or three times higher in the row next to the trees. Soil water retention at $\frac{1}{3}$ bar was also twice as high in the first row as the last. Soil moisture at the time of sampling showed a similar trend (Table 12.8). Moisture along the row nearest the trees was greater at the two depths sampled and decreased with distance from the trees. No differences were observed for P or pH.

In comparison with the field soil, substantially higher concentrations of nutrients were observed directly beneath the *Alnus* border (Table 12.7). Carbon and N were up to ten times higher, Ca and K three times higher, Mg four times higher, CEC two and one-half times higher, and water retention three times greater.

In spite of the observed soil enrichment near the trees, no differences ($p = .05$) were found in grain yield between the two border and center rows (Table 12.9). However, maize growing along the field border farthest from the trees was 12% shorter than maize in the other two sampled rows.

12.4 Conclusions

Trees are unique in their influence on agroecosystem properties because of their inherent structural characteristics and perennial growth habit

Table 12.7. Surface soil properties in a maize field at three distances from a border stand of *Alnus firmifolia* trees and beneath the tree canopy

Location	pH	C (%)	N (%)	P ₂ O ₅ (ppm)	CEC (meq/100g)	Exchangeable			Water-holding capacity 1/3bar (%)
						Ca	Mg (meq/100g)	K	
Canopy	5.5 ± .2a*	3.64 ± .6a	.256 ± .05a	5.3 ± .8a	13.6 ± 2.1a	6.6 ± 1.4a	4.0 ± .7a	.84 ± .1a	19.5 ± 2.7a
1 m	6.2 ± .2b	.85 ± .0b	.068 ± .00b	1.1 ± .1b	7.9 ± 0.3b	3.8 ± 0.2b	2.1 ± .2b	.50 ± .0b	13.6 ± 0.4b
13 m	6.3 ± .0b	.47 ± .1c	.040 ± .00c	1.0 ± .1b	6.6 ± 0.6c	2.6 ± 0.3c	1.9 ± .1b	.32 ± .0c	10.8 ± 0.9c
26 m	6.3 ± .0b	.24 ± .0d	.027 ± .00d	1.1 ± .1b	5.0 ± 0.3d	1.9 ± 0.1c	1.0 ± .1c	.28 ± .0d	6.0 ± 0.2d

* Mean values ± SE; values compared across locations without one or more common letters are significantly different at the 5% level.

Table 12.8. Soil moisture within a maize field at three distances from a border stand of *Alnus firmifolia* trees and beneath the tree canopies

Zone	Soil Moisture (% dry wt. soil)	
	0 to 15 cm	15 to 30 cm
Canopy	8.7 ± 1.42b*	13.8 ± 1.74a
1 m	14.2 ± 1.28a	15.1 ± 0.66a
13 m	10.3 ± 0.79b	12.8 ± 1.13a
26 m	2.8 ± 0.64c	6.9 ± 0.32b

* Mean values ± SE; values compared across zones without one or more common letters are significantly different at the 5% level.

(Figure 12.2). Large canopies intercept wind, precipitation, and solar radiation, as well as contribute organic matter and nutrients to the soil surface. Extensive and often deeply penetrating roots help stabilize soils and draw nutrients from soil layers inaccessible to most annual crops.

The careful selection and integration of trees can result in agroecosystems that exhibit minimal losses and more efficient use of nutrients and water, improved soil physical and chemical properties, and more benign microclimates for associated crops and livestock. This integration must be based on an understanding of just how and to what extent trees modify their environment. It also means that at the agroecosystem level, we understand how trees influence those ecological processes responsible for the maintenance and productivity of a given system. Despite the fact that the presence of overstory trees can bring about short-term crop yield reductions, as demonstrated in this chapter, longer-term agroecosystem gains may be of greater benefit. This is especially true for soil erosion and nutrient cycling processes.

Steady advances are being made in our knowledge of component relationships and system level processes within increasingly diverse agroecosystems (Willey, 1981; Lowrence et al., 1984). Relatively few of these systems, however, include a perennial component. Much has also been written regarding the influence of trees in forests and plantations (Young,

Table 12.9. Yield and height of maize growing at three distances from a border stand of *Alnus firmifolia* trees

Distance (m)	Yield*	Height (cm)
1	491 ± 88a**	237 ± 5.5a
13	618 ± 84a	48 ± 6.6a
26	554 ± 116a	211 ± 4.9b

* Yield expressed as a relative index per 4-meter transect.

** Mean values ± SE; values compared among rows without one or more common letters are significantly different at the 5% level.

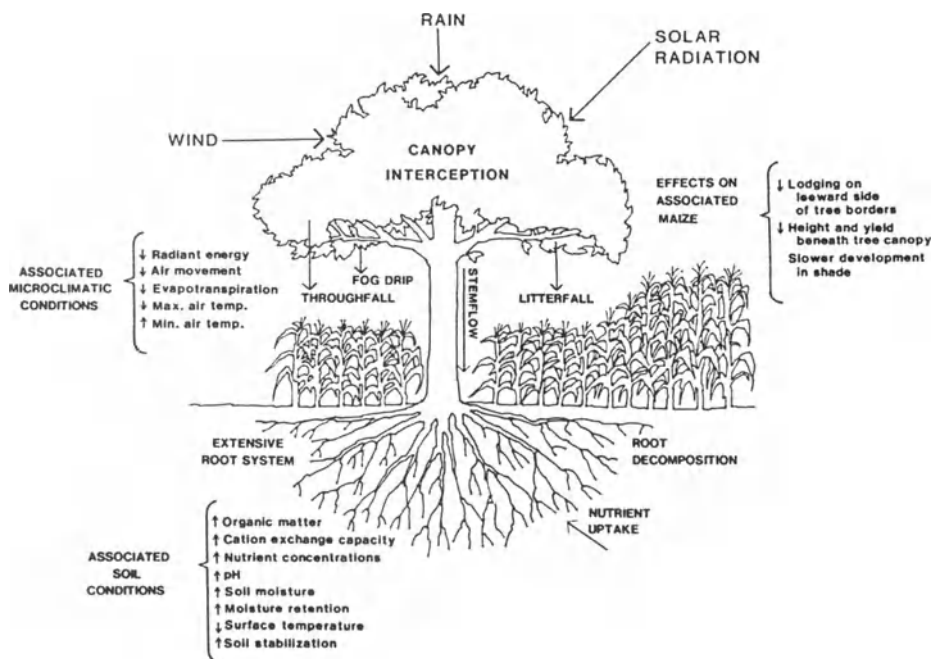


Figure 12.2. Influences of trees on agroecosystem properties in Tlaxcala, Mexico.

1986), but comparatively little is known about the role of trees in agroforestry systems (Sanchez, 1987). Research, such as the work with leguminous trees in alley cropping systems (Kang et al., 1985) and legume shade trees in coffee plantations (Glover and Beer, 1986), are notable examples of studies that further our understanding of the contribution trees make in integrated agroecosystems. Continued work in this area is essential to fully take advantage of trees as an important resource in developing a more permanent agriculture.

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13. Tree Improvement from the Ground Up: The Potential for a Select Microbial Inocula in Forestry

Tim Wood and Wm. Hugh Bollinger

13.1 Introduction

With consumption of wood and wood products increasing 1 to 2% annually in the U.S., forest industries have turned to tree improvement as a primary means of enhancing the productivity of commercial forest lands. Programs typically involve the selection and selective breeding of superior or “elite” trees, with the goal of amplifying desirable traits, such as rapid growth, good form, high wood density, and disease resistance, in the progeny. At present, most commercial breeding is accomplished through open pollination of select trees in seed orchards, and harvested seed is grown to planting stock in nurseries. In 1980, some 400 million “improved” tree seedlings were produced and planted in the U.S. (Gould, 1982). The majority of these were of high value timber species, such as loblolly pine (*Pinus taeda*), slash pine (*P. elliottii*), and Douglas-fir (*Pseudotsuga menziesii*). A small but expanding fraction consisted of fast-growing pulp and biomass species, such as poplars, alders, birches, eucalypts, and woody legumes.

Tree improvement is a long-term process. Generation times for most trees (from planting to first flowering) range from 4 to 20 years, and improvements with each generation are often small and difficult to predict. In theory, the genetic gains attainable through selective breeding are directly proportional to the selection differentials and heritabilities of target traits. Selection differential is a measure of variability within the

population and is expressed as the difference between average and select individuals. Heritability is defined as that portion of the variation that is genetically expressed through genes with additive effects. Genetic gain is calculated as the product of the two.

In practice, selection differentials and heritabilities are difficult to estimate a priori, and forest geneticists have had difficulty predicting and maximizing advances made through given crosses. This problem is particularly acute in breeding for complex traits, such as growth rate, that are influenced by numerous environmental and physiological variables (Zobel, 1971). As a result, progress in breeding trees for enhanced productivity has been scattered, and gains in growth following one generation of effort seldom exceeded 10% (Wright, 1976). Ultimate gains of 25 to 50% are likely to be attained, but for most trees this level of success will require several generations and many decades of traditional breeding (Carlisle and Teich, 1971; Reilly and Nikles, 1977).

Slow rates of progress through breeding place a premium on developing new techniques to streamline and accelerate tree improvement. Recent advances in plant morphogenesis, cellular biology, and molecular biology now offer powerful tools that may be used to shorten generation times, maximize genetic gains, and/or bypass the breeding process altogether. These tools include tissue culture, somatic hybridization, embryogenesis, and mutagenesis (Bonga and Durzan, 1982). We have been pursuing a different but complementary avenue of tree improvement, one that relies on recent advances in soil microbiology.

13.1.1 Trees as Symbiotic Organisms

Virtually all trees form symbioses with one or more groups of beneficial soil microorganisms. These microbes, also termed endophytes or micro-symbionts, include vesicular-arbuscular (VA) mycorrhizal (VAM) fungi, ectomycorrhizal fungi, *Rhizobium* bacteria, and actinomycetes in the genus *Frankia*. All directly colonize roots, enhance plant mineral nutrition, and play important roles in determining the productive capacities of their hosts.

VAM fungi are the most common of the endophytes, forming associations with most broadleaved trees and some conifers (Figure 13.1a, Table 13.1). The symbiosis is formed as the fungus colonizes the cortical cells of fine feeder roots, extends into surrounding soils, and in effect, bridges the rhizosphere, forming a fundamentally important linkage between plant and soil. The fungus obtains energy from its host in the form of fixed carbon. The plant, in turn, may benefit from:

1. enhanced uptake of phosphorus, trace metals, and other sparingly soluble nutrients (Mosse, 1973; Snaders et al., 1975; Hall et al., 1977);
2. increased drought tolerance (Safir et al., 1971; Menge et al., 1978a; Levy and Krikun, 1980; Allen et al., 1981; Hardie and Leyton, 1981);

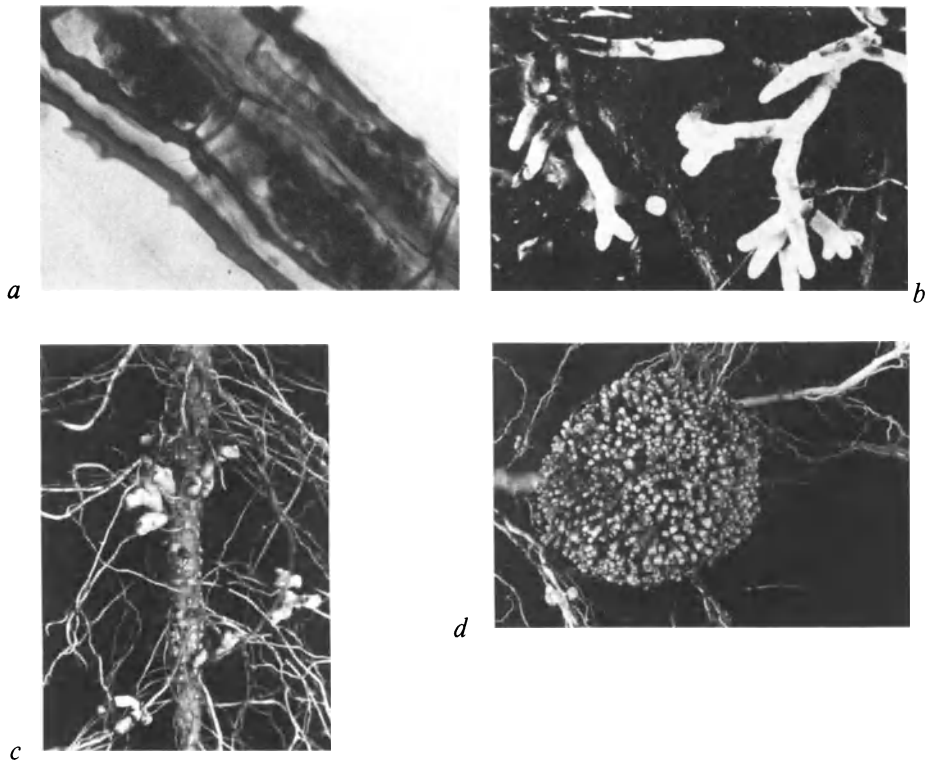


Figure 13.1. Mycorrhizal and symbiotic nitrogen-fixing associations of forest trees. a. VA mycorrhizal colonization of *Acacia pennatula*. This photo shows stained fungal hyphae and arbuscules within cleared cortical tissues of a fine root. b. Ectomycorrhizae of Douglas fir. Note the dense, white hyphal mantle surrounding the root tips (photo courtesy of J. Trappe). c. Nitrogen-fixing nodules formed by *Rhizobium* sp. on the roots of *Acacia pennatula*. d. Nitrogen-fixing nodules formed by *Frankia* on the roots of *Alnus rubra*.

3. enhanced resistance to some root pathogens (Scheck et al., 1975; Schoenback, 1978; Schenck and Kellam, 1979; Bagyaraj et al., 1979); and
4. on the average, 20 to 200% better growth, yield, and survival (see Table 13.2).

The mechanisms that underlie these benefits are not fully understood. VA mycorrhizae are thought to enhance nutrient and water uptake in large part by increasing the surface area and distribution of the root system (Bielecki, 1973; Rhodes and Gerdemann, 1975; Menge, 1981). Increases in growth, survival, stress tolerance and disease resistance may largely reflect improved mineral nutrition and water relations, but os-

Table 13.1. Mycorrhizal and nitrogen-fixing associations of some commercially important genera of trees

Mycorrhizal associate	Nitrogen-fixing associate		
	None	Rhizobium	Frankia
VA mycorrhizal fungi	<i>Acer</i>	<i>Acacia</i>	<i>Elaeagnus</i>
	<i>Liquidambar</i>	<i>Albizia</i>	<i>Casuarina</i>
	<i>Prunus</i>	<i>Leucaena</i>	
	<i>Fraxinus</i>	<i>Dalbergia</i>	
	<i>Liriodendron</i>	<i>Pterocarpus</i>	
	<i>Juniperus</i>	<i>Sesbania</i>	
	<i>Sequoia</i>		
	<i>Swietenia</i>		
	<i>Tectona</i>		
	<i>Khaya</i>		
	<i>Pinus</i>	<i>Intsia</i> and possibly other caesalpinoid legumes	
	<i>Abies</i>		
Ectomycorrhizal fungi	<i>Picea</i>		
	<i>Pseudotsuga</i>		
	<i>Tsuga</i>		
	<i>Larix</i>		
	<i>Cedrus</i>		
	<i>Carya</i>		
	<i>Betula</i>		
	<i>Fagus</i>		
	<i>Quercus</i>		
	<i>Eucalyptus</i>		<i>Alnus</i>
VA and ectomycorrhizal fungi	<i>Populus</i>		
	<i>Salix</i>		
	<i>Juglans</i>		

Source: Data from Johnston (1949), Gerdemann (1968), Meyer (1973), Redhead (1975), NAS (1979), Rose (1979), Trappe (1979), Alwis and Abeynayake (1980), Allen and Allen (1980).

motric and hormonal adjustments to VAM colonization may be involved as well (Allen et al., 1981).

Most economically important conifers and some broadleaved trees form different mycorrhizal symbioses termed ectomycorrhizae (Figure 13.1b, Table 13.1). These are distinct from VAM associations largely in anatomy and fungal taxonomy. Ectomycorrhizal fungi colonize root cortices but do not penetrate cortical cells. Ectomycorrhizal fungi generally cover the root tip with a dense, hyphal mantle (Figure 13.1b) that is not present in VA mycorrhizae. VAM endophytes are placed in a single family of zygosporic fungi (some eight to ninety species have been named to date; Trappe, 1981), whereas ectomycorrhizal fungi span a large and diverse group of Basidiomycetes, Ascomycetes, and Zygomycetes. Trappe (1962) estimates that there are over 2,000 species of ectomycorrhizal fungi.

Table 13.2. Summary of the literature review on endophyte variability

Variable	Ectomycorrhizal fungi	VA mycorrhizal fungi	Rhizobia	Frankiae
Experimental Conditions^a				
Total no. cases	44	112	73	13
No. isolates/case	5 ± 3	5 ± 3	17 ± 10	9 ± 10
Duration of expt. (mo)	8.4 ± 10.0	3.5 ± 1.7	2.4 ± 0.9	3.1 ± 1.0
Effectivity^b				
No. cases examined	32	85	55	13
Minimum effectivity (%)	18 ± 44	65 ± 189	107 ± 374	327 ± 458
Maximum effectivity (%)	90 ± 102	325 ± 891	740 ± 1524	859 ± 520
Mean effectivity (%)	55 ± 67	170 ± 346	447 ± 1016	607 ± 522
CV of effectivity (%)	86 ± 96	74 ± 52	62 ± 34	59 ± 41
Infectivity^c				
No. cases examined	12	27	18	0
CV of infectivity (%)	60 ± 46	52 ± 31	63 ± 33	—

^aMean and standard deviation values for experimental conditions used in studies of the four endophyte types.

^bMean and standard deviation values for levels of endophyte effectivity and CV of effectivity.

^cMean and standard deviation values for endophyte infectivity.

Source: Ectomycorrhizal fungi: Marx and Zak (1965), Vozzo and Hacskeylo (1971), Bowen and Theodoru (1973), Marx (1975), Linderman and Call (1977), Marx et al. (1978), Marx (1979), Molina (1979), Valdes and Grada-Yautenzi (1980), Graham and Linderman (1981), Marx (1981), Cline and Reid (1982).

VA Mycorrhizal fungi: Daft and Nicolson (1966), Mosse (1975), Schenck et al. (1975), Powell (1976), Sanders et al. (1977), Powell and Daniel (1978), Carling et al. (1979), O'Bannon et al. (1980), Abbott and Robson (1981), Daniels and Menge (1981), Davis and Menge (1981), Dhan (1981), Graham et al. (1982), Jensen (1982), Plenchette et al. (1982), Schenck and Smith (1982).

Rhizobia: Erdman (1946), Lange and Parker (1960), El Essawi and Abdel Ghattar (1967), El-Sherbeeney et al. (1977), Keyser et al. (1979), Munns et al. (1979), Bromfield and Roughley (1980), Ikram and Broughton (1980), Trinick (1980a, 1980b), Kremer and Peterson (1982).

Frankiae: Dillon and Baker (1982), Normand and Lalonde (1983), Wood and Turner (unpublished data).

Despite these differences, ectomycorrhizae function in ways similar to those described for VAM associations. Pines inoculated with appropriate ectomycorrhizal fungi, for example, typically benefit from improved uptake of phosphorus and other nutrients (Bowen, 1973), increased resistance to root pathogens (Marx, 1975; Sinclair et al., 1982), and significant gains in growth and survival (Table 13.2). Some trees in the Betulaceae, Salicaceae, and Tiliaceae form both ecto- and VA mycorrhizae associations (Gerdemann, 1968, Table 13.1).

In addition to these fungal associations, some trees form nitrogen-fixing symbioses with bacteria in the genus *Rhizobium* or actinomycetes (filamentous bacteria) in the genus *Frankia*. Rhizobial associations are largely limited to leguminous plants. Commercially important genera of leguminous trees include *Acacia*, *Albizia*, *Leucaena*, and *Sesbania*. *Frankia* fix nitrogen in association with three important tree genera: *Alnus*, *Elaeagnus*, and *Casuarina* (Table 13.1).

Rhizobia and frankiae form nodules on the roots of their hosts (Figures 13.1c and 13.1d), and within these structures they convert atmospheric dinitrogen to ammonium nitrogen (Akkermans et al., 1979; Hardy et al., 1979). In dense stands of well-nodulated legumes and alders, these bacteria can fix 200 to 500 kg N/ha/yr (NAS, 1977; Akkermans and Van Dijk, 1981), amounts equivalent to those used in forest fertilization. Because the majority of this nitrogen is passed directly to the host, many leguminous and actinorrhizal trees grow very rapidly, with plantation yields approaching 30 to 40 m³ wood/ha/yr (Smith, 1978; NAS, 1980). In fact, inoculation with appropriate bacterial strains typically speeds the growth of these trees several fold over nonnodulated controls. Most nitrogen-fixing plants also form mycorrhizal associations, and both sets of endophytes are often necessary for optimal growth (Smith et al., 1979; Rose and Youngberg, 1981; Yost, 1981).

13.1.2 Prospects for “Improved” Tree Symbioses

Because mycorrhizal fungi and nitrogen-fixing bacteria play important roles in determining the productive capacities of trees, we believe they hold considerable potential for use in forestry. This potential has been tapped in part, but applications to date have been largely corrective. Foresters have used the organisms to overcome the stunting of seedlings grown in disturbed or fumigated soils containing depauperate levels of natural inoculum (Mikola, 1973; Marks, 1977; Molina, 1977).

We propose that mycorrhizal fungi and nitrogen-fixing bacteria can do more; that their full potential in forestry goes beyond remedy and enters the realm of tree improvement. Instead of breeding and selecting for superior trees alone, foresters could engineer and select for elite symbioses, the performance of which is optimized through application of superior endophytes.

In this chapter, we explore the selection of microbial symbionts as a potentially significant and rapid stage in the tree-improvement process. We examine the functional variabilities that exist within groups of mycorrhizal fungi and nitrogen-fixing bacteria to determine whether selection differentials are large enough to warrant the search for superior strains. We also discuss the benefits and limitations that this facet of tree improvement may offer for increasing and sustaining the productivity of forest lands.

13.2 Functional Diversity Among Mycorrhizal Fungi and Nitrogen-Fixing Bacteria

In theory, the gains expected through use of superior endophytes should be directly proportional to the selection differentials in growth-promoting ability (effectivity) that exist between average and select strains. This relationship is analogous to that described for predicting advances through tree breeding, with the exception that “heritability” in effectivity is difficult to assess because there is little information concerning the performance of given fungal and bacterial strains across numerous, diverse environments. As such, our predictions of gains through endophyte selection will rest solely on deriving estimates of functional diversity among strains.

Numerous studies have shown that isolates of given mycorrhizal fungi or nitrogen-fixing bacteria differ markedly in their abilities to promote plant growth. Unfortunately, most reports compare only two to ten isolates on one or two hosts. None has provided an adequate measure of the overall variation in effectiveness that exists, for example, within the ectomycorrhizal fungi or the frankiae. The literature, as a whole, however, may be adequate and we set out to distill from this body estimates of functional variability for the four groups of endophytes.

We assumed that variation in “infectivity” (the degree to which isolates colonize a given host) and “effectivity” (the degree to which endophytes promote the growth or survival of a given host) is normally distributed within populations of mycorrhizal fungi and nitrogen-fixing bacteria. We know of only one data set that is large enough to test this assumption. Gibson et al. (1975) isolated approximately 1700 strains of *Rhizobium trifolii* over a five-year period from pastures in southern Australia. Isolates were evaluated in the greenhouse under environmentally uniform conditions for nitrogen-fixation and growth promotion in association with a single cultivar of *Trifolium subterraneum*. We compiled and standardized their results with respect to uninoculated controls (Bergerson, 1970) and found that they closely form an ideal normal distribution (Figure 13.2). Obviously this data set confirms only one instance of normality and it is difficult to extrapolate to endophyte populations as a whole.

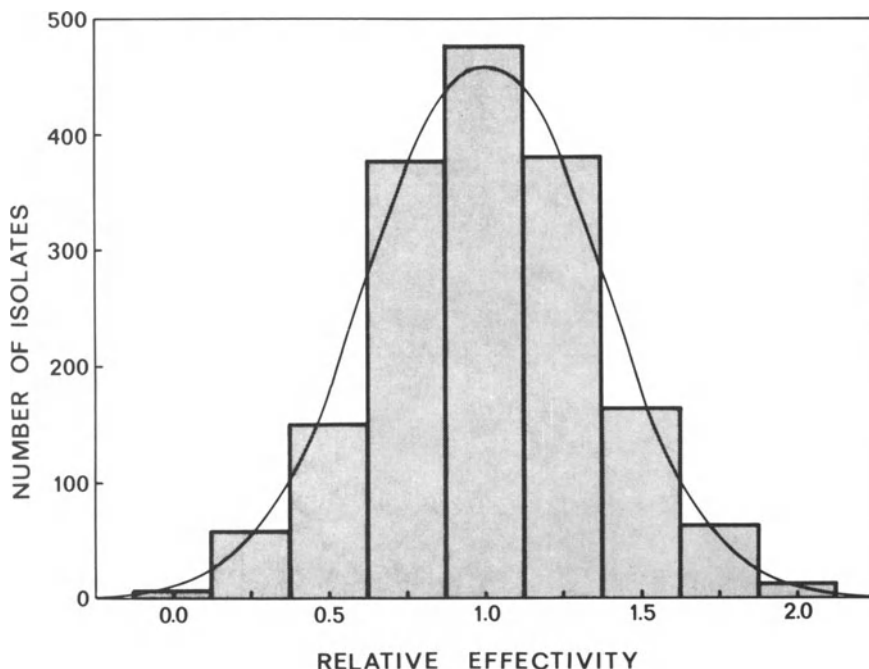


Figure 13.2. The variation in effectivity among 1700 isolates of *Rhizobium trifolii* collected from pastures in southeastern Australia was distributed in normal fashion. In this figure, the actual distribution (shaded histogram) is compared with the best fit normal curve. Skewness and kurtosis statistics for the data are negligible. Note that the abscissa has been scaled so that control values equal 0.0, and the effectivities of average isolates equal 1.0. Interestingly, the CV for these data is approximately $\pm 35\%$, or half of our grand mean estimate. This discrepancy is likely due to the fact that the authors biased their sampling against less effective strains by taking isolates only from the largest, most highly pigmented nodules near the root crown. As such, they presumably sampled a select fraction of the *Rhizobium* population.

Nevertheless, continuous biological data of this type are typically distributed in normal fashion (Sokal and Rohlf, 1969), and without information to the contrary, it is reasonable to assume that variability in endophyte performance is normal as well.

We then went to the literature and chose as our unit “case” the basic experiment in which three or more endophyte strains were tested individually on a given host under uniform environmental conditions.

We collected all studies available to us that reported such experiments. Few restrictions were placed on selection. Because of the nature of our survey, we had to assume that endophytes were chosen at random without prior knowledge of their growth-promoting abilities. If authors stated that

a given strain was used because it was particularly effective or ineffective on the intended host, the isolate and/or case were discounted. Studies had to contain data on uninoculated controls to facilitate comparisons between cases. Only studies employing single-strain inocula were chosen. We discounted cases in which multiple-strain cultures or nodule homogenates were used. Finally, we required that within a given case, standard amounts of inoculum for each strain were applied. This stipulation was difficult to verify for many studies of VAM and ectomycorrhizal fungi, and in those instances, differences in inoculum potential may have contributed to the variation noted in strain effectiveness. Cases were taken from the agricultural, horticultural, reclamation, and forestry literatures. Most studies contained more than one case because they tested a set of strains on more than one host, or ran parallel tests under several environments.

For statistical purposes, cases were divided into those measuring infectivity and those measuring effectivity. Infectivity was typically measured as percentage of root length colonized by mycorrhizal fungi, or number of nodules formed by nitrogen-fixing bacteria. Effectivity was typically measured as an increase in shoot height, plant dry weight, foliar phosphorus concentration, or total plant nitrogen.

Results for each case were standardized to allow comparisons between studies. The effectivity of each strain was calculated as the difference in performance between inoculated plants and controls. This difference was normalized as a percentage of the control value so that data on survival, growth, and nutrient content could be pooled. Variability between strains was standardized as the coefficient of variation (CV) of effectivity across all isolates tested in the case. Infectivities of individual strains could not be standardized as above because infection values for controls equaled zero. Therefore, infectivity data based on different parameters could not be pooled. But variability between strains was normalized using a CV based on absolute values of infection.

For each case that measured effectivity, we recorded endophyte type, number of strains tested, duration of the experiment, minimum, maximum, and mean host response, and coefficient of variation of host response. For each case measuring infectivity, we recorded endophyte type, number of strains tested, duration of the experiment, and coefficient of variation of absolute infection.

In all, 43 studies containing 242 cases were reviewed. The cases were compiled and divided into eight groups by endophyte type and by focus (effectivity versus infectivity). Means and standard deviations were computed for all parameters in each group.

Results of the analysis are given in Table 13.2. As background, three quarters of the cases we reviewed concerned variability among VAM fungi or *Rhizobium* bacteria, and most of these used agricultural crops as hosts. In contrast, the work with ectomycorrhizal fungi and frankiae

typically employed tree seedlings as hosts. Studies of mycorrhizal fungi averaged five strains per case, although those testing nitrogen-fixing bacteria typically compared 10 to 20 isolates (Table 13.2). Almost all studies were conducted under controlled greenhouse conditions, and in most cases, plants were grown in soils or artificial mixes that had been sterilized prior to inoculation. Most experiments ran for 2 to 6 months from inoculation to harvest.

Under these conditions, coefficients of variation in endophyte performance were comparatively uniform (Table 13.2). Mean CVs of effectivity and infectivity for the four endophyte types all fell in the range of 50 to 90%, and standard deviations typically equaled one-half to two-thirds of the means. Analyses of variance further showed that there were no significant differences at the $p < .05$ level between any two mean CVs.

In this light, we calculated a grand mean coefficient of variation, based on all 242 cases, of $68.4 \pm 51.6\%$. The 95% confidence interval about this value is 61.9 to 74.9%; or for the purposes of generalization, approximately 60 to 75%. In combining all CVs we have considered infectivity as a component of effectivity. As a measure of average endophyte variability, this mean CV can be used to predict relative differences between average and select strains if, again, the distribution of that variation is assumed to be normal.

With this assumption and our mean coefficient of variation, we constructed theoretical normal curves depicting variation in performance within an ideal population of endophytes (Figure 13.3). Two distributions are given (one based on a CV of $\pm 60\%$ and the other on a CV of $\pm 75\%$) to show the range inherent in the 95% confidence interval about the mean CV. As in Figure 13.2, the abscissa has been scaled so that the effectivity of the average isolate equals 1.0, and the standard deviation about that average equals $\pm \text{CV}/100$.

The shaded portions of Figure 13.3 represent the 5% most effective endophytes, which according to the distribution shown should be 2 to 3 times as effective as average strains. In comparison, the top 10% and top 1% of the endophytes (areas not indicated in Figure 13.3) should be 1.8 to 3 and 2.5 to 3 times as effective as average isolates, respectively.

These selection differentials are comparable to those obtained by foresters practicing mass selection of trees from unimproved stands (Wright, 1976), and they indicate the potential for significant gains in tree performance through the use of superior endophytes. The magnitude of the gains that might be realized in field trials are of course difficult to predict from the results of the greenhouse studies surveyed here. Nevertheless, the fact that considerable variation exists in endophyte performance justifies the search for superior strains.

Interestingly, the high levels of superiority predicted by our theoretical distributions (Figure 13.3) were seldom attained in the studies surveyed.

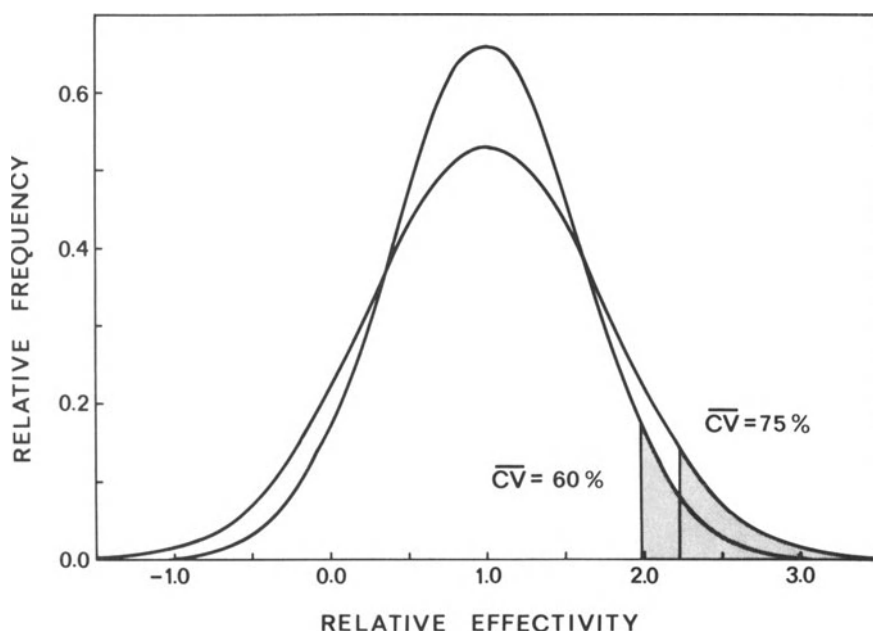


Figure 13.3. Theoretical normal curves depicting variation in effectivity among an ideal population of endophytes. The two curves bound the 95% confidence interval around the grand mean coefficient of variation in endophyte diversity that was calculated in this study. The abscissa has been scaled as in Figure 13.2. The shaded portions of the curves represent the 5% most effective endophytes in the populations. Note that roughly 5% of randomly selected isolates should be ineffective or capable of reducing host growth (see portions of curves below 0.0 on the abscissa). Negative growth responses were not evident from the statistics shown in Table 13.2, but fully 30% of the cases reviewed had minimum effectivities of less than 0.0.

Maximum effectivities for mycorrhizal fungi and nitrogen-fixing bacteria averaged 1.4 to 1.9 times, not 2 to 3 times the mean effectivities (Table 13.2). This discrepancy may indicate that our estimates are overestimates, biased because, for example, workers tended to select endophyte strains for study that they knew differed markedly in growth promotion ability. Or the discrepancy may result from the fact that relatively few strains per case were tested, and that the chances of selecting a truly superior endophyte were small. In the following section we will explore the latter possibility.

13.3 Strategies for Selecting Superior Endophytes

Mycorrhizal fungi, rhizobia, and frankiae can be obtained from established culture collections, but at present, the numbers of isolates available

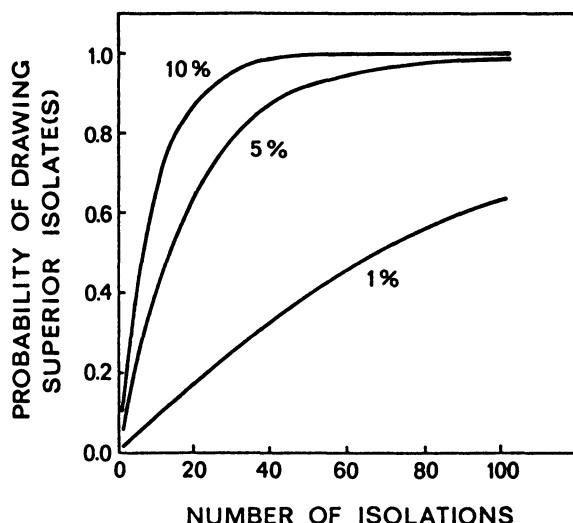


Figure 13.4. The probability (P) of drawing at least one superior isolate at random from a population of endophytes is a function of the degree of superiority required (X = top 10%, 5%, or 1%) and the number of isolations made (Z). The curves shown here are based on the probability function: $P = 1.00 - (100 - X/100)Z$.

for use in forestry are small. Their full natural diversity has not been tapped, and continued collections from the field are warranted. Are there means of identifying *a priori* superior endophytes in the field?

We know of few. Sampling can be concentrated in the region intended for inoculum use to guarantee that strains are adapted to target climates and soils. Organisms can be collected from roots, nodules, and surrounding soils of intended hosts to reduce chances of collecting incompatible isolates. Some rhizobia can be isolated from prominent pink nodules near root crowns to maximize chances of obtaining strains that are infective and effective (Gibson et al., 1975). In addition, acetylene reduction assays can be run on *Rhizobium* and *Frankia* nodules prior to isolation to ensure reasonable nitrogenase activities (Benson, 1982). Aside from these guidelines, however, collections must be made virtually at random, without prior knowledge of strain performance.

In this context, drawing superior isolates becomes a matter of chance, and questions arise concerning how many organisms must be isolated at random to obtain an elite strain. Figure 13.4 plots this probability function for endophytes in the top 10%, 5%, and 1% of their population. It shows, for example, that 60 isolates must be collected to ensure with 95% confidence that at least one strain among the 5% most effective is obtained. If only 50% confidence is required, 14 isolations can be made, although if 99% confidence is required, some 90 isolations are necessary. The sampling effort also increases with the level of superiority demanded

(see companion curves in Figure 13.4). At the upper extreme, to ensure with 99% confidence that at least one strain among the 1% most effective is drawn, some 500 isolations are required (not shown in Figure 13.4).

These numbers of isolates are far greater than the five to twenty strains that have typically been tested in studies of endophyte diversity (Table 13.2), and with good reason. It is an enormous task to evaluate the performance of hundreds of symbiotic bacteria and fungi when greenhouse and field evaluation, lasting months to years, are involved. Unfortunately, there are no good alternatives to greenhouse and field trials at this time, but clearly a premium exists on developing rapid *in vitro* tests and biochemical assays for predicting *in vivo* performance.

13.4 Applications of Microbial Inocula in Forestry

For the past two decades, the major efforts at increasing yields of wood products from forest lands have been agricultural in nature. The trend has been towards intensively managed plantation systems employing genetically superior planting stock; extensive site preparation; broad scale applications of fertilizers, pesticides, and herbicides; as well as mechanical planting and harvesting techniques. Results have been dramatic in some instances. Under intensive management, maximum annual yields of Douglas-fir and loblolly pine, for example, have been increased 70% and 300%, respectively, over unmanaged forests on comparable sites. (Farnum et al., 1983). These advances have not been made without the added costs associated with tree improvement, site preparation, and chemical inputs. As a result, intensive plantation forestry is economically justified only for high-value timber and pulp crops grown on favorable sites. And even in these situations, questions of sustainability remain.

Tree improvement, in and of itself however, is not as limited in application. Planting stock can be selected and bred for maximum yield on marginal lands where extensive site manipulations are economically untenable. Furthermore, once seed orchards are established, superior tree genotypes are no more expensive to produce and plant than unimproved stock.

Superior microbial inocula, as elements of tree improvement, also have broad applications in forestry. Mycorrhizal fungi and nitrogen-fixing bacteria are important components of forest ecosystems, central not only to the growth and vigor of trees, but also to the maintenance of soil fertility and nutrient cycles (Trappe and Fogel, 1977; Bowen, 1980). As such, they hold tremendous potential for use as biological complements and alternatives to elements of intensive forest management. Selection, production, and application of elite inocula will, of course, involve added expense, but costs should be more than offset by the following benefits.

1. *Enhanced production of planting stock in nurseries:* Production of containerized seedlings and bareroot stock can be improved through the application of mycorrhizal fungi and nitrogen-fixing bacteria (Trappe, 1977; Kormanik, et al., 1982). Benefits are typically most apparent when artificial potting media are used, nursery beds are fumigated, or natural inocula are otherwise absent. Incorporating microbial inocula into nursery practice may require that cultural practices be altered, but potential savings through improved growth, greater crop uniformity, diminished disease problems, and reduced numbers of culls can more than offset the costs associated with the inoculum and its application. We estimate for example that use of VAM fungi in our container plant nursery will reduce production costs by 15 to 20% per plant under commercial operation.
2. *Enhanced survival of outplanted stock:* Transplant is frequently a tenuous stage in the reforestation process. Bareroot and containerized seedlings with limited root systems are particularly susceptible to drought, disease, and nutrient deficiencies. Inoculations with mycorrhizal fungi and nitrogen-fixing bacteria can counter these stresses, improve transplant success by 50% or more, and reduce restocking costs (Johnson and Crews, 1979; Cooper, 1981; Menge, 1982).
3. *Improved growth of tree seedlings during establishment in the field:* Because pre-inoculated seedlings carry their symbionts to the field, they do not wait 1 to 6 months following transplant for natural associations to develop and become functional. Instead, they grow more continuously through the establishment period and frequently enjoy 20 to 200% better growth than noninoculated plants during the first and second years in the field (Planchette et al., 1981). Improved growth and vigor during this establishment period can reduce requirements for weed control, reduce losses from herbivory (Janos, 1980), and diminish restocking costs.
4. *Reduced requirements for stand fertilization:* Because mycorrhizal fungi and nitrogen-fixing bacteria fundamentally enhance plant mineral nutrition, they can be used to offset or eliminate the need for chemical fertilizers. Again, well nodulated alders and woody legumes in fully stocked stands can fix hundreds of kilograms per hectare of nitrogen annually (NAS, 1977; Akkermans and Van Dijk, 1981). VA mycorrhizal inoculations have been shown to offset by 60 to 80% or more the phosphorus, nitrogen, and trace metal fertilizer requirements of some tree crops (Menge, 1981).
5. *Long-term acceleration of tree growth:* Few studies have followed the growth of inoculated versus uninoculated trees over extended periods, and the potential for long-term growth enhancement is uncertain. Outplanting studies with ectomycorrhizal pines in Australia and the United States have shown that the absolute growth differences between inoculation treatments that develop during years 1 and 2 following

outplanting are typically maintained or widened during years 3 through 5 (Theodorou and Bowen, 1970; Marx, 1980). In some cases, these results can be ascribed to continued differences in the mycorrhizal status of the trees, but we suspect a more general phenomenon is being observed. Differences in size and relative growth rate between trees in the early life of a stand are typically maintained through time and can account for much of the variation in stand structure and yield 15 to 30 years later (Wakeley, 1971; Autry, 1972). In theory, then, inoculations with superior mycorrhizal fungi and nitrogen-fixing bacteria that maximize tree growth during establishment could result in increased yields at harvest.

To date, ectomycorrhizal inoculations, those used most extensively in forestry, have proven most effective on planting stock destined for adverse, severely disturbed sites or for areas otherwise lacking in suitable endophytes (Mikola, 1973; Marx, 1977; Molina, 1977). Responses to inoculation have been less consistent in more routine situations, such as the reforestation of clearcuts, where conditions can be intermittently harsh, but where relatively intact populations of indigenous endophytes provide natural inoculum (Molina, 1977; Marx, 1980; Kropp, 1981).

Applications of elite inocula will continue to be valuable for reforestation of marginal lands, but their potential uses are much broader. Our analyses suggest that effective endophytes for poor, average, and favorable sites can be found. Substantial variability exists within populations of mycorrhizal fungi and nitrogen-fixing bacteria, and with sufficient effort, superior strains, some two to three times as effective as average strains, will likely be found. The task of tapping and applying this natural diversity represents an exciting opportunity towards realizing a more productive and sustainable forestry base.

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14. Variability, Stability, and Risk in Intercropping: Some Theoretical Explorations

John Vandermeer and Brian Schultz

14.1 Introduction

Reviews and bibliographies of intercropping and multiple cropping are not difficult to come by (e.g., International Rice Research Institute [IRRI], 1974, 1975; Papendick, et al., 1976; Sanchez, 1976; Kass, 1978; Willey, 1979, 1979a, 1981; Lamberts, 1980; Beets, 1982; Steiner, 1984; Govinden et al., 1984; Francis, 1986; Vandermeer, 1988), and chronicle an immense quantity of research in all corners of the globe on an incredible diversity of crop combinations. One might thus expect an excellent data base to have been accumulated along with something of a solid theoretical framework, given the ubiquity of the phenomenon and quantity of scientific attention it has received. But neither an excellent data base nor a well-accepted theoretical framework is evident. The practice of intercropping is apparently more complicated than monocultural production and has been resistant to the development of a central core of theory that might guide empirical work. Consequently, the voluminous empirical literature is eclectic, scattered, and sometimes confusing. This vast empirical base has led to only modest gains in our ability to understand extant systems.

Our view is that the absence of a solid theoretical framework within which empirical work can be interpreted has been the major cause of this failed empiricism. In response to this view, a general theoretical focus has recently been put forth by one of us (Vandermeer, 1988). Two core ideas dominate in this theory. First, when one species has an effect on

the environment that causes a negative response in the other species, yet both can more efficiently utilize necessary resources when living together than when in monoculture, we have the *competitive production principle* (or the “interference” production principle) (Vandermeer, 1981), or simply “reduced competition.” Second, when the environment of one species is modified in a positive way by a second species, such that the first is facilitated by the second, we have the *facilitative production principle* (Vandermeer, 1984), or simply facilitation. The vast majority of examples of intercrop advantage cited in the literature fall into one or the other of these two categories. Thus, for example, the partitioning of the nitrogen environment (e.g., Snaydon and Harris, 1979), in which a legume uses atmospheric nitrogen and the grass uses soil nitrate, is an example of reduced competition, whereas the reduction of herbivore attack, as a consequence of the presence of a disruptive crop (Risch et al., 1983), is an example of facilitation.

Although most of the proposed mechanisms of intercrop advantage fall within this dichotomous classification, there is one factor that clearly does not, and thus requires special treatment. That factor is reduced variability, and the development of a theoretical basis for its study is the purpose of this chapter. A frequently claimed advantage of intercropping is its capability of dealing with environmental variability, implicitly equivalent to the avoidance of risk (Reich and Atkins, 1970; Abalu, 1977; Francis and Sanders, 1978; Reddy and Willey, 1981). Indeed, intercropping reviews commonly contain sections on variability and risk (e.g., Aiyer, 1949; Norman, 1974; Kass, 1978; Willey, 1979; Lamberts, 1980; Mead and Riley, 1981), yet only rarely is the subject a central focus. Three notable exceptions are contained in the work of Rao and Willey (1980), Pearce and Edmondson (1982), and Schultz (1984). The latter work specifically treats the first two, and forms the basis of a later section.

Ecologists have long been concerned with variability and/or stability, especially with reference to their relationship to diversity (e.g., May, 1974; Goodman, 1975; Murdoch, 1975; McNaughton, 1977). It has generally been thought obvious that diverse systems are more stable, or less variable than more monotonous ones. It was, and still is, a common-sense notion, which is why May's (1974) claim of the reverse was such a surprise. All things being equal, according to May, a more diverse system should be less stable, not more. Although May's definition of stability was perhaps too restrictive for many ecologists, his conclusion was nevertheless a stimulating one, and led to much intense discussion and debate.

With this background of ecological theory, it is tempting to make an analogy to intercropping systems. Two species growing together is indeed a more diverse system than either one growing alone. But most of the theoretical formulations from ecology implicitly deal with questions of great diversity, tens or hundreds of species, and the qualitative and quan-

titative conclusions they draw are not likely to bear much fruit when applied to intercropping systems.

Yet a similar common-sense notion regarding diversity and stability seems to have evolved independently in the intercropping literature. For example:

- “In traditional agriculture, mixed cropping has usually dominated, . . . largely for risk reduction.” (Norman, 1977),
- “In subsistence agriculture, . . . it (intercropping) is an insurance against total crop failure.” (Beets, 1982),
- “In intercropping systems net income advantages appear to be secondary to risk reduction, . . .” (Lynam et al., 1986).

In these examples, and in the many others that could be cited from the intercropping literature, only minimal if any evidence is mustered in favor of the claim. The consensus seems similar to earlier notions held by ecologists—diverse systems (intercrops) must be more stable than monotonous ones (monocultures). As we note below, there is neither empirical data nor an underlying theoretical rationale that would justify such an expectation.

In what follows, we first consider some special problems in the evaluation of yield variability (or what is frequently referred to in the agronomic literature as yield stability). This is followed by a general theoretical treatment of yield variability under competitive and facilitative production. Finally we approach the topic from the point of view of the structure of the environment and the farmer’s decision-making process. More elaborated forms of this material can be found in Schultz (1984) and/or Vandermeer (1988).

14.2 Problems of Measurement and Evaluation

Intercrop advantage with regard to variability of yields is a more complicated subject than with regard to the means of yields. Six variables must be taken into account: monoculture yield of crop 1, monoculture yield of crop 2, the combined yield of two monocultures, yield in intercrop of crop 1, yield in intercrop of crop 2, and combined intercrop yield. Each of these variables has an associated variance, and our interest is in two different forms of comparisons. First, the variability of crop 1 in an intercropping situation is compared to what it is in monoculture, and second, the variability of the combination in intercrop (the “system” variability) is compared to what it is in the system of both monocultures. Both of these comparisons are interesting generally and speak to the question of variability in intercropping. Yet they are independent questions, and can easily have opposite answers.

A convenient measurement of variability is the coefficient of variation (the standard deviation as a proportion of the mean), because most applications are mainly concerned with the relative variability. Although we see no objection to this measure, the literature is not so clear on exactly what is to be compared to what. With respect to which comparisons should be made when asking questions about relative variability, Rao and Willey (1980) made the first significant stride forward. They compared the variance of the sum of the intercrop yields to the variance of the sum of the monoculture yields, where the monocultures are assumed to make up exactly the same proportion of the total as was obtained in the intercrop. So, in their example, they assumed that the monocultures were made up of 61% sorghum and 39% pigeonpea, thus making the yields correspond exactly in both monoculture and intercrop (i.e., the proportions of the total yield attributable to sorghum was the same in the intercrop and in the monoculture). Using this criterion they found that the intercrop was less variable than the monocultures, thus corresponding to the conventional wisdom.

However, in the same sense that we must use optimal monoculture yields when computing land equivalent ratios (e.g., Vandermeer, 1988), we really ought to use optimal monoculture combinations when evaluating the stability (variability) of an intercrop, rather than fixing the monocultures at other proportions. That is, if the goal is to determine whether the intercrop is less variable than monocultural alternatives, we ought to use those monocultures that show, as monocultures, the lowest variability possible. Let us suppose that of the available land, a fraction p is planted with crop 1 and a fraction $(1-p)$ is planted with crop 2. The problem is to determine what exact p will give the minimum coefficient of variation.

First note that for two crops x and y , it is true by definition that:

$$\sigma_{x+y}^2 = \sigma_x^2 + \sigma_y^2 + 2\rho_{x,y} \sigma_x \sigma_y, \quad (1)$$

$$\mu_{x+y} = \mu_x + \mu_y, \quad (2)$$

and

$$\sigma_{kx}^2 = k^2 \sigma_x^2; \mu_{kx} = k \mu_x \quad (3)$$

where σ_{x+y}^2 is the variance of the sums of monocultural yields for each site, $\rho_{x,y}$ is the correlation coefficient between x and y , k is a constant, and σ^2 and μ are the variance and mean, respectively. Now let k equal p for one crop and $(1-p)$ for the other crop in equation 3. Substituting equation 3 into equations 1 and 2, we may write the coefficient of var-

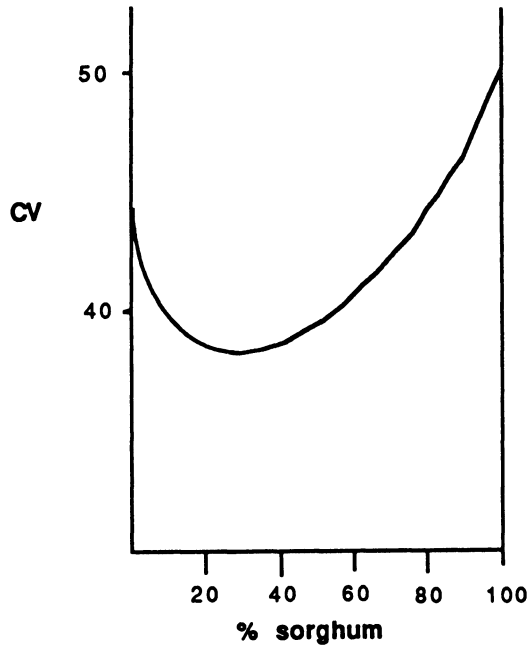


Figure 14.1. The relationship between coefficient of variation and percentage of area in sorghum monoculture. From data of Rao and Willey (1980).

iation of the total yields for a given mix of monocultures (p of crop 1 and $1-p$ of crop 2) as,

$$CV_{x+y|p} = \frac{[p^2\sigma_x^2 + (1-p)\sigma_y^2 + 2p(1-p)\rho_{x,y}\sigma_x\sigma_y]^{1/2}}{p\mu_x + (1-p)\mu_y} \quad (4)$$

This theoretical relationship between p and the coefficient of variation is plotted in Figure 14.1 for the original data of Rao and Willey (1980). As can be seen, the fraction of land planted to sorghum that would give the minimal coefficient of variation is about 20%, a much smaller value than the 61% amount originally used. Also in that figure, the actual values of the coefficient of variation for the intercrop are plotted, showing that the intercrop is only apparently less variable than the monocultures. If one makes the comparison with the minimally variable monocultural combination, the intercrop would appear to be more variable.

It is possible to compute exactly the proportions of monocultures that would give the minimal coefficient of variation. By differentiating equation 4 with respect to p , equating it to zero, and solving for p , we obtain the proportion of crop 1 expected to result in the monocultural combi-

nation with the minimal total coefficient of variation, or p^* . Thus, we have,

$$p^* = \frac{\mu_x \sigma_x^2 - \mu_y \rho_{x,y} \sigma_x \sigma_y}{\mu_y \sigma_x^2 + \mu_x \sigma_y^2 - (\mu_x + \mu_y) \rho_{x,y} \sigma_x \sigma_y} \quad (5)$$

If $p \geq 1$, then 100% of crop x is the least variable "combination," and of $p^* \geq 0$, 100% of crop y is least variable. For the original data of Rao and Willey, the computed value of p^* is .23. The combination of 23% sorghum to 77% pigeonpea results in a coefficient of variation of 37.6%, which is less variable than any of the combinations originally analyzed by Rao and Willey, including the intercrop. Further details may be found in Schultz (1984).

It is also true that some other intercrop might be less variable than the one actually studied. Indeed, if we were to require that both the intercrop and monocultures are those that give minimal variance, we must insist that even in this most carefully documented case, the question of whether or not the intercrop is more stable (less variable) is yet undecided.

We here ignore the question of risk, which depends on mean yield values as well as variability (Rao and Willey, 1980; Pearce and Edmondson, 1982). Although risk is usually of more practical interest to producers, relative variation allows us to examine intrinsic variation independent of the many factors that affect mean yields, such as the acreage grown of a given crop.

14.3 The Origin of Variability in Intercrops

Although the evaluation of yield stability as an empirical problem is quite complicated and as yet unresolved, nevertheless, a great deal can be said theoretically about how variability is generated and what its pattern might be as a function of various biological and cultural forces. In this section, we explore the necessary consequences of competitive and facilitative production in terms of variability. More details of these developments can be found in Schultz (1984).

The yields of any monoculture will vary over time and space. Let us for the moment ignore whether the variation is over time or space, and simply ask how would that variation appear if we had two crops and plotted their yields on a graph of one against the other. Such a representation is provided in Figure 14.2a. A cloud of points will be observed: a large cloud if the variability is relatively large and a small cloud if the variability is relatively small. For purposes of the qualitative developments sought here, it is convenient to think of the magnitude of the

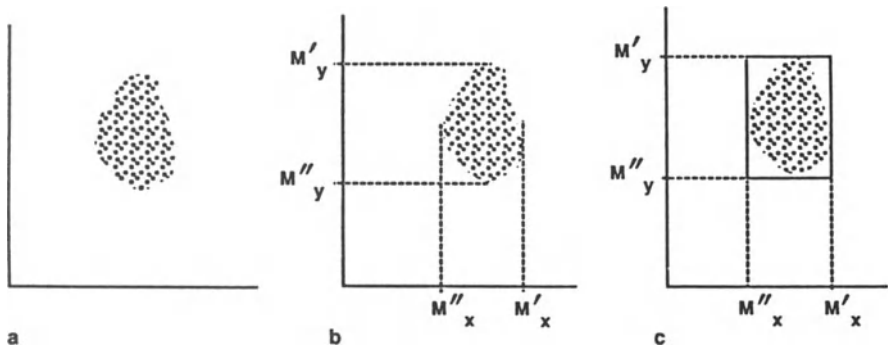


Figure 14.2. Cloud of points of yield of crop 1 plotted against yield of crop 2, illustrating the construction of the “envelope”, which represents the cloud of points (a). The rectangle M'_y , M'_x , M''_x , M''_y in (b), defines the rectangle that is the envelope of the cloud of points in (c).

variability as being directly proportional to the magnitude of the cloud of points.

It is a simple matter to identify the extreme values along each axis, as has been done in Figure 14.2b. In this example, we can expect the yield values for the crop on the x axis to be somewhere between M'_x and M''_x , and the yield values of the crop on the y axis will be somewhere between M'_y and M''_y . These extreme values can thus be thought of as defining a rectangular area within which the cloud of points will be found. This area is called the monocultural envelope, and refers to the rectangular outer limits of the actual yields of the monocultures, as pictured in Figure 14.2c.

Note that the cloud of points need not be symmetrical within the envelope. For example, in Figure 14.3, there are two examples of non-symmetrical clouds within the same envelope. If the underlying forces causing the variability affect the two crops in a similar way, the expectation is that the two will vary more or less in the same way. Thus, there will be a general positive correlation between their yields, as pictured in Figure 14.3b. But it is equally plausible to suggest that the underlying forces have opposite effects on the two crops, thus generating a negative correlation, as depicted in Figure 14.3a. We shall have cause to return to these correlations in a moment.

The cloud of points representing the monocultural yields will be reduced on both axes through competition. Thus, in Figure 14.4a, we present the cloud of points for a tomato/cucumber system (Schultz et al., 1982), including both the monoculture and intercrop clouds. The expected points are reduced according to the amount of competition experienced. But here, because we began with variability in the monocultures, that variability is likewise reflected in the intercrop. Consequently,

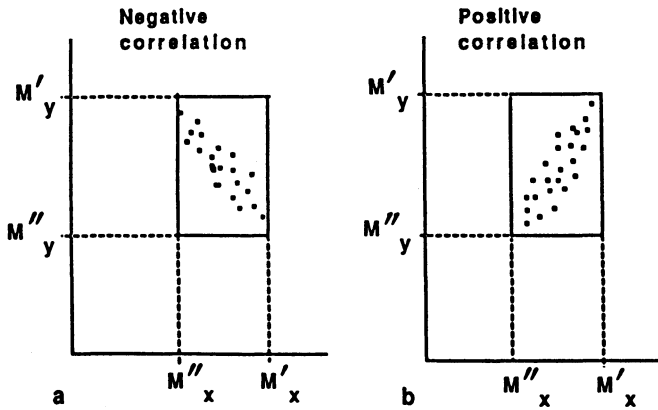


Figure 14.3. Illustration of position of empirical points when correlation between yields is negative (a) or positive (b).

to compare relative variation, it is necessary to translate the monoculture envelope from its original position to a position in which its center (that is, the point representation of the two average monocultural yields) corresponds to the center of the intercrop cloud, retaining the same exact coefficient of variation that existed in the original monoculture envelope. A convenient method for accomplishing this transformation graphically is with the range and median of the cloud of points. Although the standard measurement of relative variation is the coefficient of variation (standard deviation divided by the mean), there is no reason why the ratio of the range to the median should not be used. For theoretical and heuristic purposes, that measure is useful here. Taking the ratio between the range and median as our measure of the relative variability of the system, it is a simple task to translate the monocultural envelope to a position in which its center is on the center of the intercrop cloud, reducing the size of the envelope such that the new envelope retains the relative variability of the original monoculture envelope. This new envelope is the "equivalent" monoculture envelope. It represents the limits on a cloud of points that have the identical relative variability as the monocultures, but with the mean values reduced to be equivalent to the intercrop yields. In Figure 14.4b, the original monoculture envelope is scaled down so as to have its center on the intercrop means, retaining its initial relative variability. As can be seen, the cloud of points representing the intercrop falls almost exactly inside of the equivalent monocultural envelope. Had the intercrop cloud been different, the conclusions could have been different. For example, in Figure 14.5, theoretical examples are presented where the intercrop cloud (the shaded area) is such that the cucumber variability is greater; but the tomato variability less in the intercrop (Figure 14.5a), or the reverse (Figure 14.5b), or the total variability is less (Figure 14.5c).

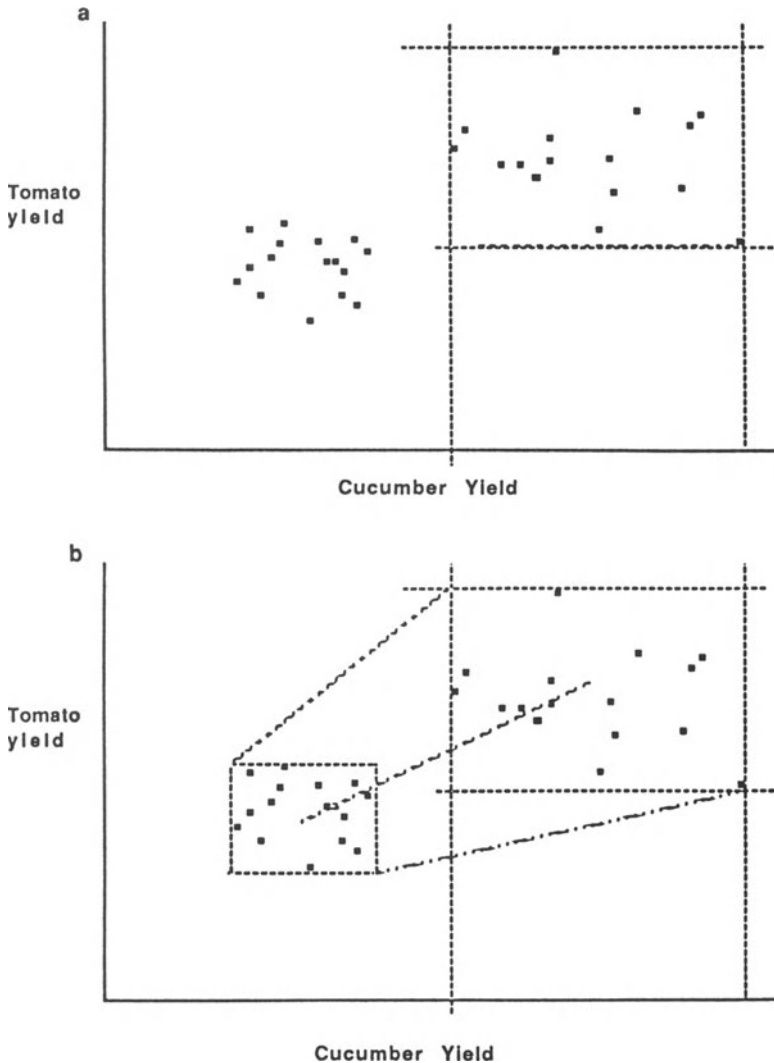


Figure 14.4. Monocultures and intercrops of tomato and cucumbers (x -axis is cucumber yield). a. Raw data with monoculture envelope sketched in. b. Construction of scaled monoculture envelope compared with the empirical data of the intercrop.

Note that this method is virtually identical to comparing the coefficients of variation between monoculture and intercrop. It has the advantage that it is easily visualized graphically and, what is most important here, facilitates a further qualitative theoretical development.

The next problem is to construct the theoretical cloud of points representing the intercrop yields. That cloud of points, as already described,

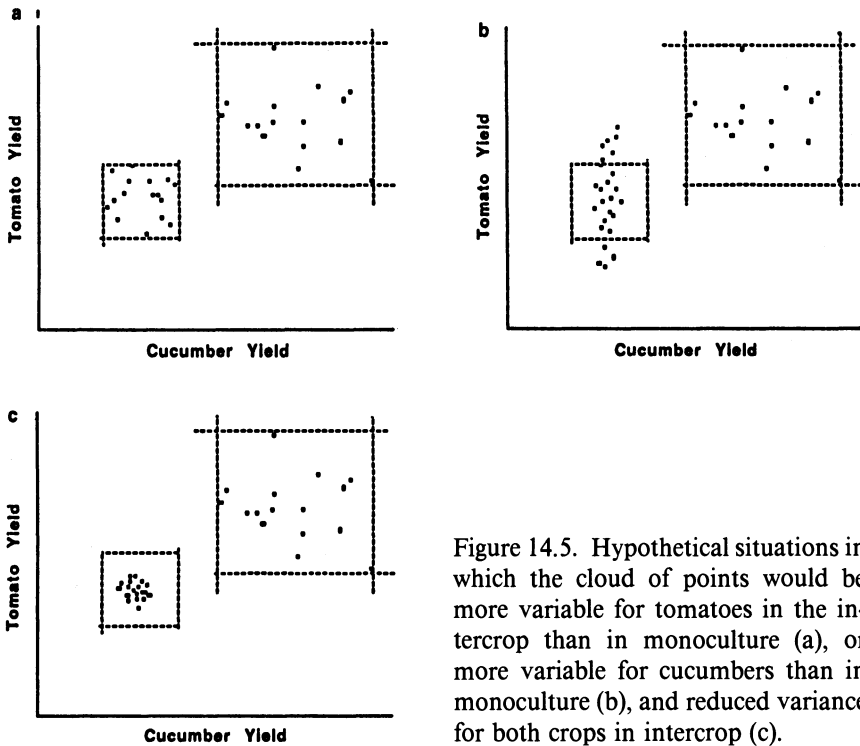


Figure 14.5. Hypothetical situations in which the cloud of points would be more variable for tomatoes in the intercrop than in monoculture (a), or more variable for cucumbers than in monoculture (b), and reduced variance for both crops in intercrop (c).

must be less than (on both axes) the cloud of points representing the monocultural yields, presuming that the process of competition is operative. For simplicity of presentation, we presume that the interaction function is linear, such that the yields of the two crops are related to one another as,

$$\begin{aligned} y &= M_y - ax \\ x &= M_x - by \end{aligned} \quad (6)$$

where x and y are the yields in the intercropping situation, a and b are the competition coefficients, and M_y and M_x are the monocultural yields. Assuming that all of the environmental variability occurs in the monocultures (i.e., the interaction coefficients remain invariant), we obtain the pattern shown in Figure 14.6. The two functions are linear, and their variability is represented as a series of parallel lines, the extremes of which are shown in Figure 14.6a. Under this set of assumptions, if we translate the monocultural envelope so that its center is positioned at the center of the intercrop envelope and it retains its original coefficient of variation, the translated monocultural envelope will be exactly inscribed in the intercrop envelope, as shown in Figure 14.6b.

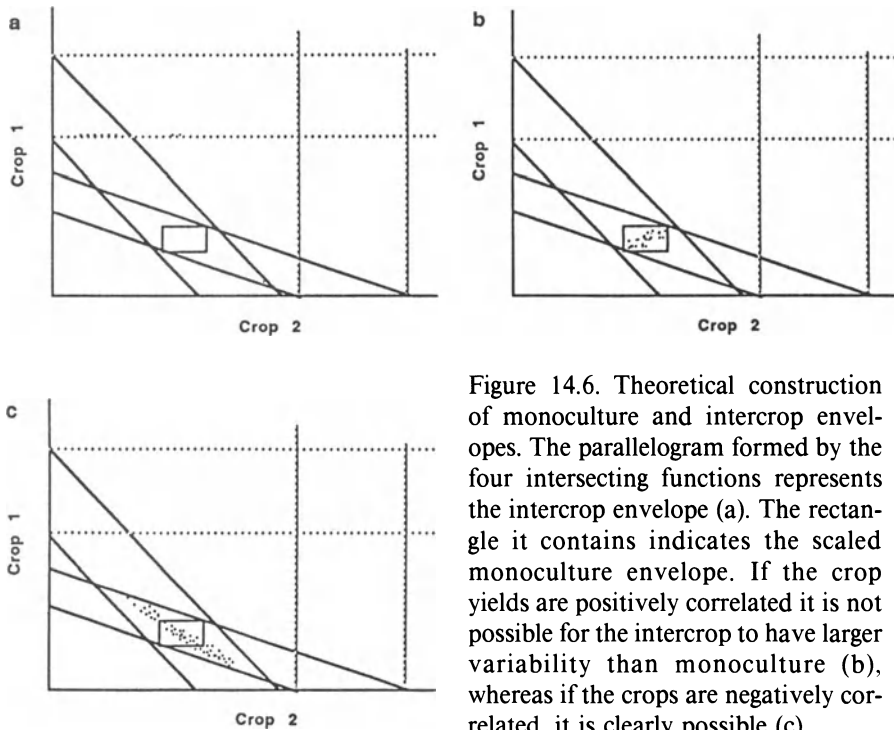


Figure 14.6. Theoretical construction of monoculture and intercrop envelopes. The parallelogram formed by the four intersecting functions represents the intercrop envelope (a). The rectangle it contains indicates the scaled monoculture envelope. If the crop yields are positively correlated it is not possible for the intercrop to have larger variability than monoculture (b), whereas if the crops are negatively correlated, it is clearly possible (c).

With this representation, we can deduce two very important facts. First, because the monocultural envelope is inscribed inside of the intercrop envelope, it is not possible for the monoculture to be more variable than the intercrop, in terms of either the component intercrop variabilities, or the variability of the total yield. This conclusion is profoundly at odds with the conventional wisdom that intercrops are less variable than monocultures, suggesting not only that it is not logically necessary for intercrops to be less variable than monocultures, but that it is not even possible for them to be so. Second, as pictured in Figure 14.6, depending on the correlation between the crop yields, the yield of each individual intercrop can be either equivalent to the monocultures or greater than them, in terms of variability. Specifically, if the crops are positively correlated (Figure 14.6b), the variability of the monocultures (again either in terms of individual components or the total) and the variability of the intercrops are expected to be nearly identical. But if the crops are negatively correlated (Figure 14.6c), then each intercrop is expected to be more variable than its corresponding monoculture.

The above graphical model can be formalized as follows. Let the monocultures of species i range from M_i to M'_i , and the median be $M_i = (M_i + M'_i)/2$. The mean intercrop yields are symbolized as y^* and x^* , and are given by the solution to equations 6, which are,

$$\begin{aligned} y^* &= (M_y - aM_x)/(1 - ab) \\ x^* &= (M_x - bM_y)/(1 - ab). \end{aligned} \quad (7)$$

The relative variability of the monocultures will be $(M'_i - M_i)/M_i$. Thus to retain the same relative variability for the intercrop we require,

$$\frac{M'_x - M_x}{M_x} = \frac{R_x}{x^*} \quad (8)$$

in which R_x is the length of the equivalent monoculture envelope, along the x -axis. Solving the R_x using equation 7, we obtain,

$$R_x = \frac{(Mx' - Mx)(Mx - bMy)}{M_x(1 - ab)}, \quad (9)$$

and the corresponding equation for y . the area (and thus the joint relative variability) of the equivalent monoculture envelope is $R_x R_y$, or,

$$V_m = R_x R_y = \frac{(Mx' - Mx)(Mx - bMy)(My' - My)(My - aMx)}{M_x M_y (1 - ab)^2} \quad (10)$$

Presuming the linear model as described above, we compute the area of the intercrop envelope, which we take as proportional to the intercrop variance, as,

$$V_I = \frac{(M'_x - M_x)(M'_y - M_y)}{1 - ab} \quad (11)$$

The intercrop relative variability will be smaller than that of the monoculture when $V_I < V_m$, or, after simplification,

$$bM_y^2 + aM_x^2 < 0 \quad (12)$$

which is impossible as long as all the terms are positive. We are thus forced to the conclusion that, as long as only competition is operative, intercrops will tend to be more variable than monocultures, both in terms of the variabilities of individual components and in terms of the variability of the combination.

Using equation 12 we can quickly extrapolate the exact opposite conclusion in the case of double facilitation (mutualism). If both a and b are negative (as they would be in the case of mutualism), it is not possible for the intercrop to have a larger relative variability than the monoculture, whereas in the case of single facilitation (a positive and b negative), the apportionment of relative variability will depend on the relative sizes of aM_x^2 and bM_y^2 . We thus obtain the generally surprising result that in-

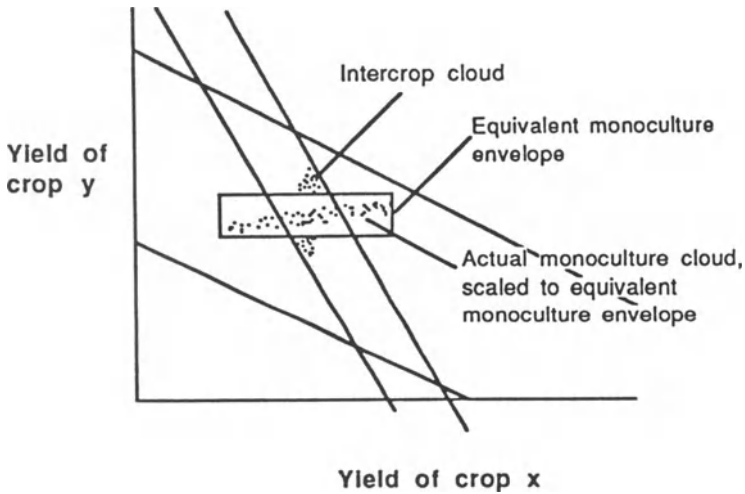


Figure 14.7. Decreased intercrop variability caused by large differences in variability in the two crops.

tercrop relative variability will tend to be larger than that of the monocultures if competition is the main operative force, whereas intercrop relative variability will tend to be smaller when facilitation is the main operating force.

But these results are all based on the underlying assumption of the linear model, including the tacit assumption that the monocultural points will be relatively symmetrically shaped as they are in Figures 14.4, 14.5, and 14.6. If the intercrop produces a correlation between the yields of the two species, the intercrop cloud of points is restricted to only a subset of the intercrop envelope. As shown in Figure 14.7, it is conceivable to obtain an intercrop relative variability that is smaller than that of the monoculture if the correlations between yields are positive. Such a possibility is especially likely when the relative variabilities of the two monocultures are very different. Schultz (1984) gives the exact conditions for such a result.

Schultz (1984) presents several other modifications of the above arguments that can theoretically lead to intercrops having lower variances than the monocultures. For example, if the competition coefficients are nonlinear, and the yields are correlated with respect to the environmental variability (e.g., as in Figure 14.6a), it is possible to have a lower variance in the total yields from the intercrops. Similarly, if the competition coefficients are positively correlated with the yield potentials as both vary through time, it is again possible, but not necessary, to find intercrop variability lower than that of the monocultures.

But even with such modifications, the general conclusion seems to be that under a competitive model, intercrops will tend to be more variable than monocultures, as has been assumed by the conventional wisdom (but see Marshall and Brown, 1973). On the other hand, the opposite is true for a mutualistic model, with an intermediate situation for a single facilitation model. Because the conventional wisdom of reduced variability in intercrops does not seem to be supported by available evidence, nor is there a theoretical reason for expecting it to be generally true, it seems that a more reasonable null hypothesis would be that intercrops will tend to be more variable than monocultures if competition is operative, and that they may be either more or less variable when facilitation is operative.

14.4 The Potential Set, Adaptive Function, and Risk Aversion

Under facilitation, a special form of analysis sheds considerable light on the question of optimal intercrop strategy under a risk-averse, decision-making system. There are two distinct concepts that come together to form this special analysis. First is the biology of the plants themselves, as represented in the *potential set*, which could be “convex” or “concave” (as explained below). Second is the *adaptive function*, which varies qualitatively depending on the decision strategy and the nature of the environment. We consider first the notion of the potential set.

14.4.1 The Potential Set

Suppose that bean yields are affected negatively through competition with maize, in an environment in which a critical bean pest (e.g., a beetle) is absent. But suppose also that there is an alternative environment in which the beetle is at its maximum possible abundance. In this alternative environment, the competitive effect on the beans is overwhelmed by the positive effect of the maize deterring the beetle through some mechanism, such as drawing predators into the system, or confusing the beetle’s host-finding behavior. As stated above, we are looking at both the competitive “effects” and the facilitative “effects” of the added species, and we have two environments: one in which the competitive effect of the secondary species dominates (when the beetle is absent), and one in which the facilitative effect dominates (when the beetle is present).

So, for different densities of the “secondary species” (in this case maize), we stipulate a pair of yields for the primary crop: the yield in environment 1 (with the beetle) and the yield in environment 2 (without the beetle). If the facilitative production principle is to be operative in the first place, the shape of the primary crop yield versus secondary crop density should be monotonically increasing in environment 1, and mon-

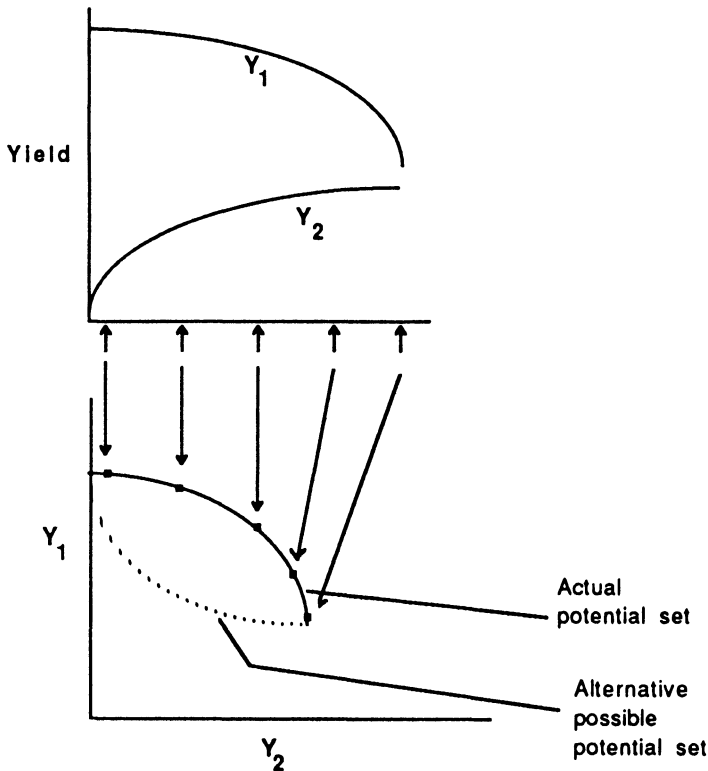


Figure 14.8. Construction of the potential set from yield curves. The yields in the top graph are plotted against different intensities of the secondary crop species.

otonically decreasing in environment 2. Naturally, if only competition operates, both curves are monotonically decreasing, and the following analysis does not apply.

The potential set is the collection of yields and is represented as a graph of the yields, that is, “yield in environment 1” versus “yield in environment 2.” In Figure 14.8 such a graph has been constructed from the graph of yield of primary crop versus density of secondary crop. This graphical representation of the yield set makes a very crucial distinction possible. Suppose the yields had fallen along the dotted line in the figure as opposed to where they in fact are. The obvious difference in the shape of the set indicated by the solid line and the set indicated by the dotted line suggests the simple dichotomous classification of convex (solid line) versus concave (dotted line) sets. This distinction is important in terms of planning an intercropping system.

14.4.2 The Adaptive Function

In the current example, we have defined two environments: very high beetle density and very low beetle density. From the point of view of the

bean plants, how are these two environments viewed? What fraction of the time will the plant be exposed to each alternative?

To answer this question accurately, we must take into account the question of environmental grain, a topic covered below. For now, an approximate answer is that, from the plant's point of view, if the population density of the beetle is one-half of its maximum value, it is identical to having the maximum population density of the beetle but operating only one-half of the time. A hundred beetles eating for one-half of a day is the same as fifty beetles eating all day (obviously not strictly true, but useful here as a simplifying assumption).

Thus, any real environment (e.g., some particular population density of beetle between the maximum and minimum) can be approximated as a fraction of the two environmental extremes. To compute the yields with the different maize densities, where one-half of the time the beetle is absent and one-half of the time it is at maximum density (or in fact is always exactly half way between maximum and minimum density), we employ the equation,

$$Y = .5y_1 + .5y_2 \quad (13a)$$

where Y is the mean yield and y_1 and y_2 are the yields in the two environments. This equation is called the *adaptive function*. We can rearrange it so that y_1 is expressed as a function of y_2 , as follows,

$$y_1 = 2Y - y_2. \quad (13b)$$

In Figure 14.9, this equation is plotted for various values of y . The intent is to maximize the value of y , which is to say we are looking for the largest value of the principle crop yield possible, given the constraints of the potential set. We see how this process operates by plotting Figures 14.8 and 14.9 together, as is done in Figure 14.10. The point at which the adaptive function is tangent to the potential set is the point of optimal design for the intercrop.

But what might be the result if, instead of the two environments occurring 50% of the time each, one of them occurred 80% of the time and the other 20% of the time? Instead of .5 for the constants in the adaptive function, the constants would equal .8 and .2. In general, if environment 1 occurs p of the time, and environment 2 occurs $1-p$ of the time, the adaptive function is,

$$Y = py_1 + (1 - p)y_2 \quad (14a)$$

or,

$$y_1 = (1/p) Y - [(1-p)/p] y_2 \quad (14b)$$

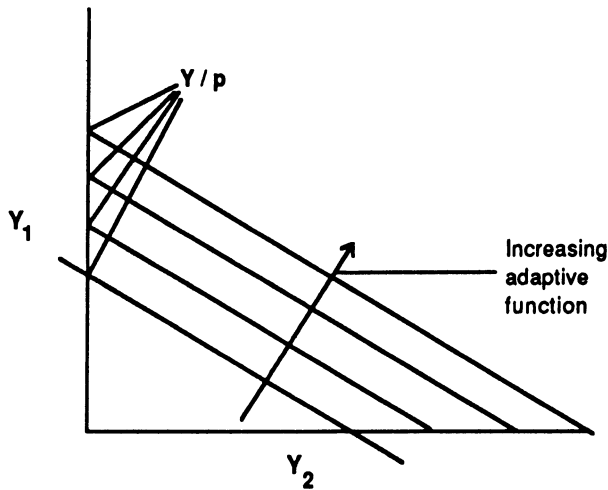


Figure 14.9. Examples of different adaptive functions.

With this generalization, it is apparent that the slope of the adaptive function changes as the proportions of the two environments change. This fact leads to interesting consequences, depending on the shape of the potential set.

Figure 14.11 illustrates the two qualitatively distinct cases. In Figure 14.11a, the potential set is convex. The optimal solution goes from a very

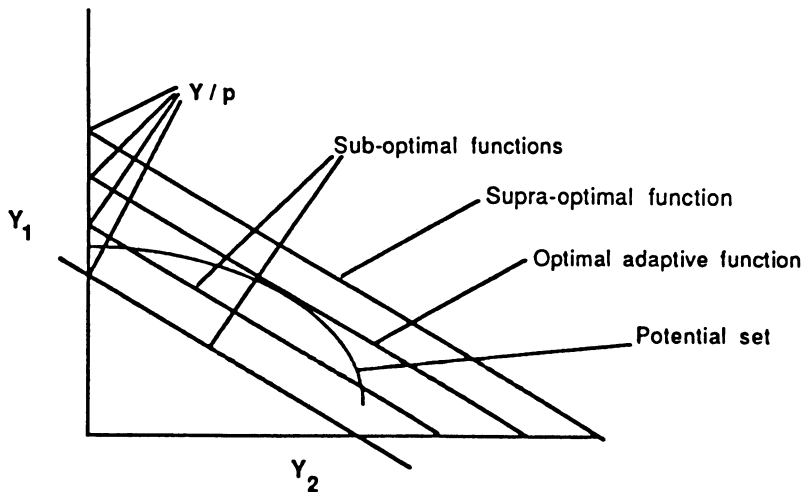


Figure 14.10. Optimizing the system with a linear adaptive function on a convex potential set.

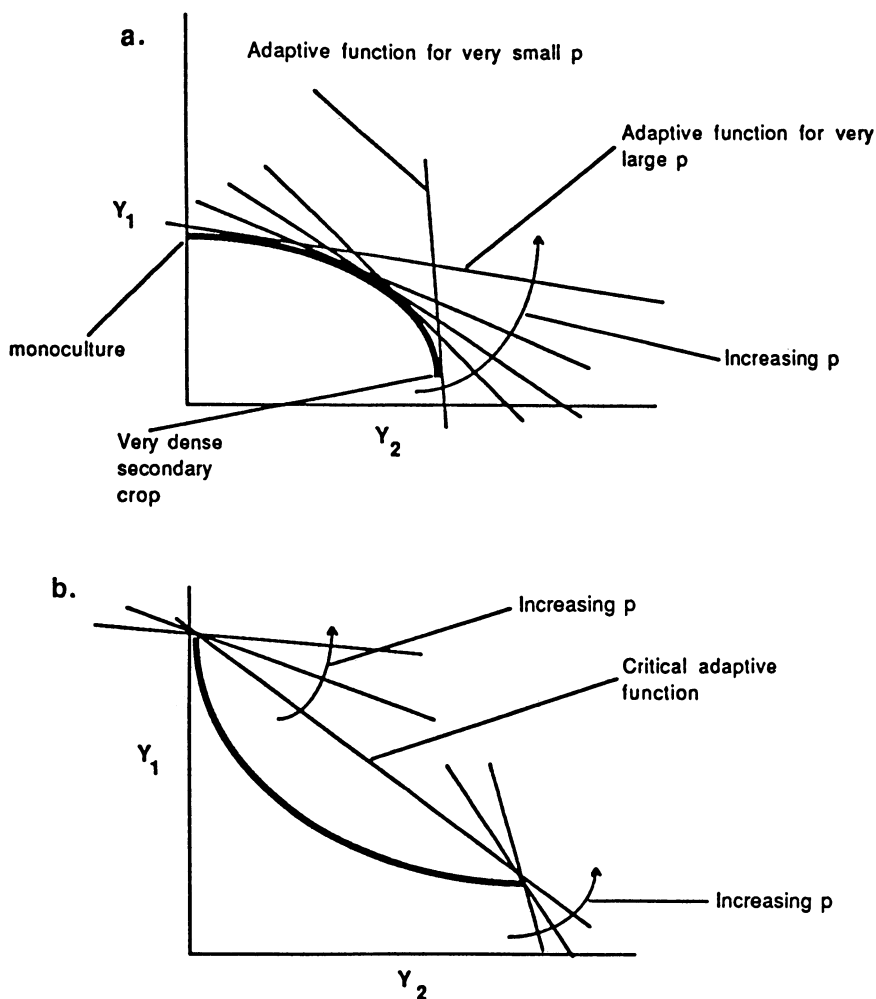


Figure 14.11. Changes in optimal solution as a function of changing environment (represented as change in p). a. Changing optimum on a convex potential set. b. Changing optimum on a concave set.

dense planting of the secondary crop, through less dense plantings of the same crop, eventually reaching a monoculture, depending on the mix of the two environments. The situation is qualitatively different if the potential set is concave, as pictured in Figure 14.11b. As the mix of the two environments changes, the optimal solution remains at the dense secondary crop, to a critical point, after which there is a sudden switch to the monoculture as optimum. Thus, whether or not an intercrop will be optimal depends, not only on the presence of the facilitative environment, but also on the shape of the potential set.

Next, we consider the set of factors that causes a producer to choose one system or another. These factors are many and varied, but can be conveniently summarized in two broad categories: those factors that are sought (high yields, profits, etc.) and those factors that are avoided (yield below some critical level, a critical low value of marginal profit, etc.). For example, a typical midwestern U.S. farmer who chooses to grow grains is choosing to accept a low, but relatively assured profit. A neighboring farmer who grows tomatoes or pickles is choosing to accept a relatively high chance of losing everything, but also seeking the high profits that sometimes come with these crops. The first farmer seeks to avoid the risk, the second to maximize profits. These two relatively distinct strategies dictate, at least in part, the choice of cropping systems.

In all that follows, we presume that a producer attempts either to maximize something (usually yields or profits) or minimize something (usually risk of losing capital investment). For convenience, our analysis continually refers to yields, although the entire development could equally refer to profits or other decision factors. We have thus far analyzed maximizing the yield of a principal crop, and we now turn to minimizing the risk of falling below a critical yield of that crop.

14.4.3 The Adaptive Function Under Risk Minimization

The first optimization criterion considered was yield optimization, in which the adaptive function was linear. These results can be conveniently reviewed in Figures 14.10, 14.11a, and 14.11b. We now turn to the alternative decision criterion, risk minimization. When dealing with the problem of risk minimization, it becomes important to note the pattern or grain of the environment.

One of the ways in which different environmental patterns can be categorized is in the dichotomous classification of “fine grained” versus “coarse grained.” In a coarse-grained environment, each distinct patch of the environment occurs in an all or nothing fashion, from the point of view of an individual in the population. Thus, a field composed of patches of high phosphorous and other patches of low phosphorous would be coarse grained if an individual plant experienced either a high phosphorous or a low phosphorous patch during its lifetime. If the patches are so small that an individual plant embeds its root mass into numerous patches of each type, the environment is fine grained. Although in the real world, environmental patterns most undoubtedly lie somewhere on a continuum between fine and coarse, for heuristic purposes, it is convenient to analyze only the extremes, the black or white alternatives of the coarse-grained case versus the single, gray alternative of the fine-grained case.

Consider the first fine-grain situation. Suppose that a minimum possible yield exists (referred to as min), probably zero in most practical

situations, but here considered to be some positive value, for the sake of generality. Likewise, there is some maximal value (referred to as max), usually equal to the yield of the monoculture in the competitive environment, but here considered to be some constant, again for the sake of generality. There will be some critical value of the yield, intermediate between the maximum and minimum. We presume that yields below this critical value are unacceptable. The problem then is to compute the probability of avoiding the region below the critical value, over a long time period.

Assuming variability in the system, an expected yield that is close to the maximum is unlikely to produce a value below the critical value. An expected yield that is close to the minimum is very likely, eventually, to produce a value below the critical value. Assuming that the relative position of the expected yield between max and min is equal to the probability of successfully avoiding the crash (i.e., falling below the critical value), we have, for the competitive portion of the environment,

$$\frac{Y_1 - \min}{\max}$$

and for the facilitative portion of the environment,

$$\frac{Y_2 - \min}{\max}$$

as the probability of success in each of the two environments. Then the probability of success over the whole environment must be simply the average of the probability of occurrence of the two environments (by the definition of fine grained), or,

$$p_n = \left[\frac{p(Y_1 - \min)}{\max} + \frac{(1 - p)(Y_2 - \min)}{\min} \right]^n \quad (15)$$

Because this is the probability of success over 1 year, the probability of success in 2 consecutive years will be p_s^2 , in 3 consecutive years, p_s^3 , and in n consecutive years, p_s^n . Thus, the probability of avoiding a crash for n consecutive years (p_n) is,

$$p_n = \left[\frac{p(Y_1 - \min)}{\max} + \frac{(1 - p)(Y_1 - \min)}{\max} \right]^n \quad (16a)$$

which can be altered algebraically to read,

$$p_n^{1/n} \max + \min = pY_1 + (1 - p)Y_2. \quad (16b)$$

If we allow $A = p_n^{1/n} \max + \min$, we have,

$$A = pY_1 + (1 - p)Y_2, \quad (17)$$

which is qualitatively identical to equation 14a, the adaptive function under yield maximization. Thus, the optimization procedure in a fine-grained environment is essentially the same for either a yield maximization procedure or a risk minimization procedure. The various conclusions drawn for yield maximization earlier are thus identical for risk minimization.

In a coarse-grained environment, we are concerned with year-to-year or patch-to-patch probabilities, but the same probabilities as presented above. Thus, if year 1 is a competitive environment, the probability of avoiding the crash is $(Y_1 - \min)/\max$. In year 2, suppose that again the environment is competitive. The probability of avoiding the crash for both years is $[(Y_1 - \min)/\max]^2$. Now suppose that in the third year the environment is facilitative. The probability of avoiding the crash for three consecutive years is then $[(Y_1 - \min)/\max]^2 [(Y_2 - \min)/\max]$. In general, the probability of success for n years running will be,

$$p_n = [(Y_1 - \min)/\max]^{pn} [(Y_2 - \min)/\max]^{(1-p)n} \quad (18a)$$

and the adaptive function is,

$$A = p_n^{1/n} = \left[\frac{Y_1 - \min}{\max} \right]^p \left[\frac{Y_2 - \min}{\max} \right]^{(1-p)} \quad (18b)$$

Equation 18b thus represents the adaptive function for risk aversion in a coarse-grained environment. Contrary to previous cases it is not linear in Y_1 and Y_2 , but rather follows a hyperbolic form, as illustrated in Figure 14.12.

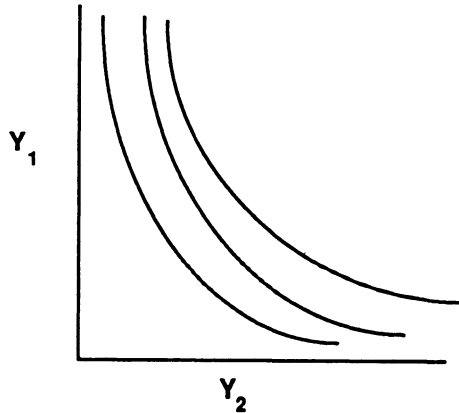


Figure 14.12. Examples of coarse-grained/risk-averse adaptive functions.

14.4.4 The Optimization Problem

Simple optimization procedures on a convex potential set follow the same pattern as with a linear adaptive function, as pictured in Figure 14.13. When p is large (a competitive environment) the optimal strategy is the monoculture. As p decreases, the optimal strategy moves along the edge of the potential set, and the optimal system slowly moves toward the position of full intercrop. Finally, when p becomes very small, the optimal is the full intercrop.

To analyze the same situation with a concave potential set, we make use of the original approach for such systems developed by Levins (1968). As shown by Schultz (1984), it will sometimes be the case that the optimal system for the avoidance of risk will be a combination of monoculture and polyculture, the so-called "mono-poly" solution. It is possible to visualize all possible combinations of systems as the *extended potential set* (equivalent to Levins' (1968) extended fitness set). That is, suppose 50% of the cultivated area is planted with a monoculture and 50% with the full intercrop. The yield of the entire area then will be 50% monoculture and 50% full intercrop. Graphically, this point is halfway between the points of the monoculture and the full intercrop (Figure 14.14). All other possible combinations of full intercrop and monoculture can be represented on the line connecting the monoculture with the full intercrop (Figure 14.14).

If we thus seek to maximize the adaptive function, free from the restraint of using only one system, we will find the largest value of the

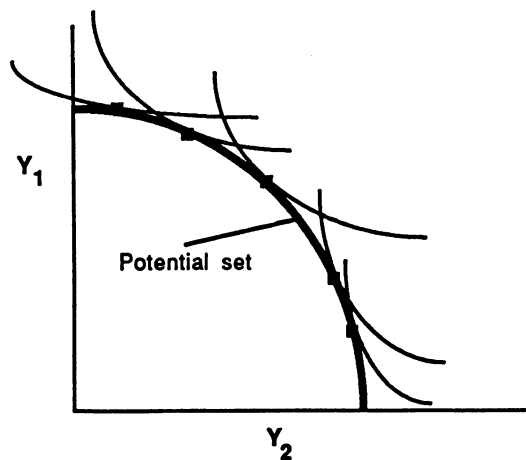


Figure 14.13. Optimizing the system on a convex potential set with a coarse-grained/risk-averse adaptive function.

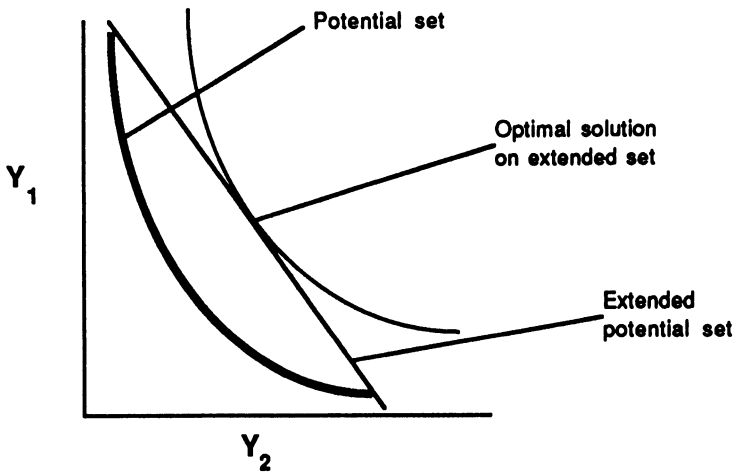


Figure 14.14. Optimizing the system on a concave potential set with a coarse-grained/risk-averse adaptive function—the “mono-poly” solution.

adaptive function that intersects the extended potential set. As can be seen from Figure 14.14, that solution will almost always be some mono-poly solution, that is, some combination of the two extremes. Thus, when the environmental grain is coarse and the producer operates under a risk-minimization criterion, and the potential set is concave, the best solution is to plant some land in monoculture and some in intercrop.

This latter result is, at first glance, a surprising and nonintuitive one. The theory suggests that when a secondary crop is highly competitive, it should only be combined with the principal crop when it affords a very good facilitative environment. But if the facilitative environment occurs in an all-or-nothing fashion (i.e., is coarse grained), it makes sense in the long run to plant some intercrops (for the years when the facilitative environment occurs), and some monocultures (for the years when the competitive environment occurs). Under these circumstances, it is better in the long run to take a loss on one of the plantings but gain big on the other, than to take a loss every p th year on the monoculture or accept lowered yields $(1-p)$ of the time in the intercrop.

14.5 Discussion

The traditional view of intercrops includes a strong bias that they somehow reduce variability and risk. We find this view unsupported by either empirical evidence or theoretical reasoning. Indeed, when analyzed carefully, the opposite can be suggested. Intercrops are likely to be more variable (and sometimes more risky as a result) than monocultures.

But it is clear that the underlying biological rules that determine the intercropping pattern are important in determining what will be the pattern of variation. Theoretically, in a strictly competitive situation, the intercrop should be more variable and more risky than the associated monocultures, whereas in a mutualistic situation, the intercrop should be less variable than the associated monocultures. Although such conclusions are based on linear approximations to the biological forces involved (competition, facilitation, or mutualism), we believe that relaxing the linear assumption generally does not alter the overall qualitative picture.

The situation in which we would expect variability to be smaller in the intercrop is that involving facilitation. When facilitation is operative, it is possible to formulate the problem in such a way that the optimal situation is at least in principle calculable. The optimum depends not only on the underlying biology of the facilitation but on the pattern (grain) of the environment that is involved in the facilitative mechanism and on the decision-making strategy of the farmer. The conclusions of this theoretical approach broadly parallel that of the simple, linear approach in that the stronger the facilitative effect, the more probable it is that an intercrop will reduce risk. Furthermore, under certain circumstances, it is clear that the optimum solution is a combination of monocultures and polycultures, the so-called mono-poly solution.

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2. Agroecosystem Design and Management

15. Reducing the Risk: Some Indications Regarding Pre-Hispanic Wetland Agricultural Intensification from Contemporary Use of a Wetland/Terra Firma Boundary Zone in Central Veracruz

Alfred H. Siemens

15.1 Introduction

In most of the numerous wetlands scattered over the lowlands of Central Veracruz, Mexico, one can trace the remains of canals and planting platforms, which are commonly called drained or raised fields (Siemens, 1980). A total of some 2,000 hectares of such patterned wetland has been located in a discontinuous band that stretches some 75 km from the hill land southeast of Laguna Mandinga, northwestward, just behind the port of Veracruz and up to the Rio Actopan. These features cannot be attributed to recent or historic land use; they must pertain to precontact epochs of agricultural intensification.

Wherever such features are found, they are considered to have been a vital complement to swidden, a manifestation of agricultural intensification. Central Mexico's still barely functioning *chinampas* have often been cited as an analogue for the raised fields but they probably embody a level of sophistication in water control and crop management that was not reached in central Veracruz. Moreover, the vestiges in the wetlands of these and other lowlands of Mesoamerica indicate a range of features and activities. The canals would have been cut to various depths and the

platforms built up to various heights. The function of the canal system would have been drainage early in the dry season and storage for scoop irrigation and fertilization later on. The complexes would have been usable for varying periods—from the dry season only to year-round. They also vary in form; some are strictly rectilinear and indeed coherently oriented, others are much less regular (Siemens, 1983). The microenvironmental context, chronology, functions, and interrelationships of all of these variants are under continuing investigation (Siemens et. al, 1988). Of interest here is a particular perspective on the system.

In January 1981, the author and several colleagues from the Instituto Nacional de Investigaciones sobre Recursos Bióticos (INIREB) attempted to clarify the topographic expression and vegetational concomitants of an apparently rudimentary complex of canals and fields. These had been sighted from the air in a wetland near El Palmar, a village about 40 k northwest of the port of Veracruz (Figures 15.1 and 15.2). Dense hydrophytic vegetation in standing water barred the way. Instead, attention was directed to a mosaic of small fields reaching down to the edge of the swamp. It was soon apparent that this was an instance of dry-season agriculture on land subject to seasonal inundation—not often noticed in rural central Veracruz, a landscape dominated by ranching and commercial, mechanized agriculture. This kind of agriculture is reported, however, from numerous other parts of Mesoamerica and elsewhere in the American tropics. Dry-season cropping, of course, is also widely practiced when rainfall permits on *terra firma*, immediately following a wet season crop in the same field. This will be left largely out of consideration here.

The manner of the encounter near El Palmar juxtaposed the actual dry-season cropping of that year with adjacent remnants of more intensive ancient and potentially related agriculture. The first of these is to be described here as seen during that initial ground survey and brief subsequent field checks, as well as overflights in 1980 and 1983. It is interesting for the hypotheses regarding the evolution of wetland agriculture, particularly in its early phases. It is considered here as an analogue, not so much in its actual crops or the details of current practice, but in the strategy it represents.

This early and rather speculative inquiry has since been followed up by Alba González Jácome and several collaborators. Valuable historical materials as well as numerous detailed observations of current agricultural practice and related aspects of community life have been introduced into the discussion. As might be expected, the 1981 situation has been shown to have been more complicated than was initially perceived; much has changed since then, as well. Further joint investigation is planned. El Palmar is likely to yield data helpful not only for the clarification of agricultural intensification, but also microaltitudinal relationships in the

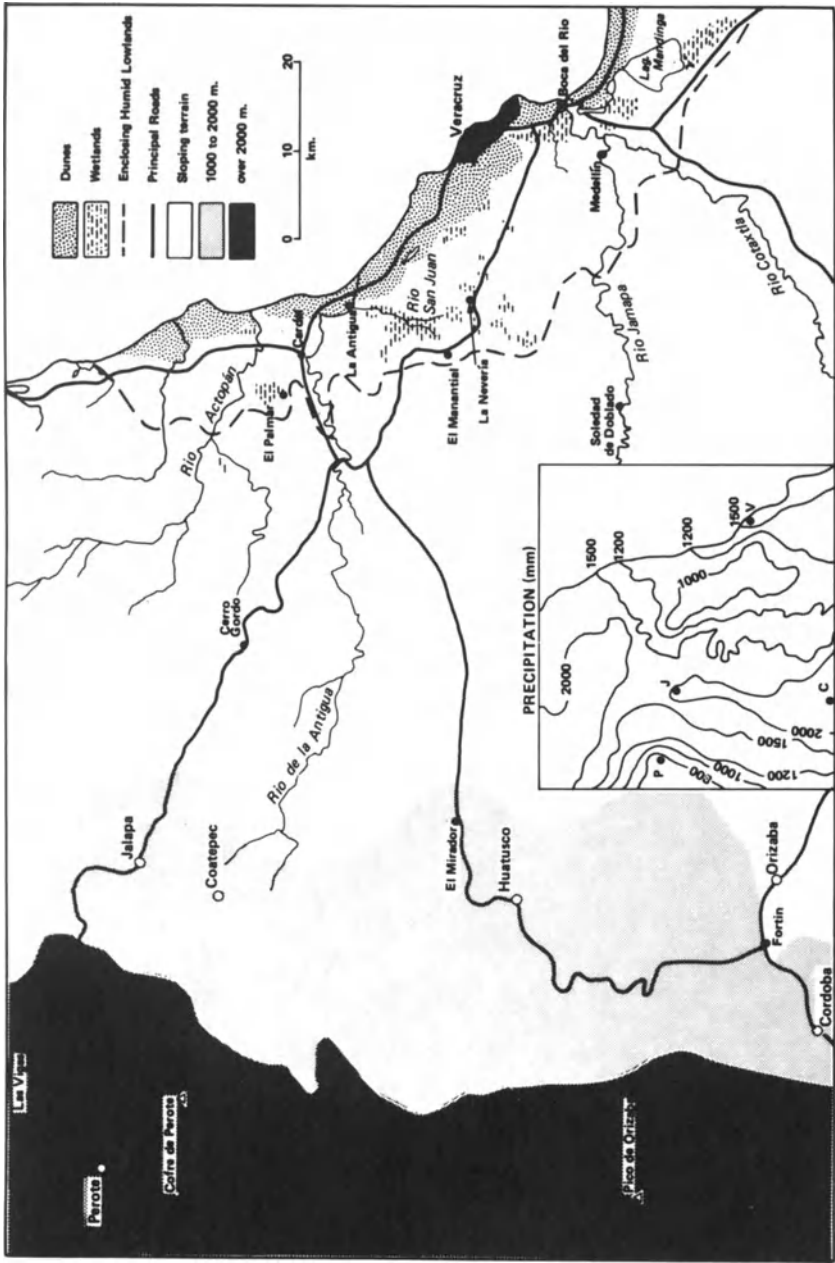


Figure 15.1. The wetlands of central Vera Cruz.

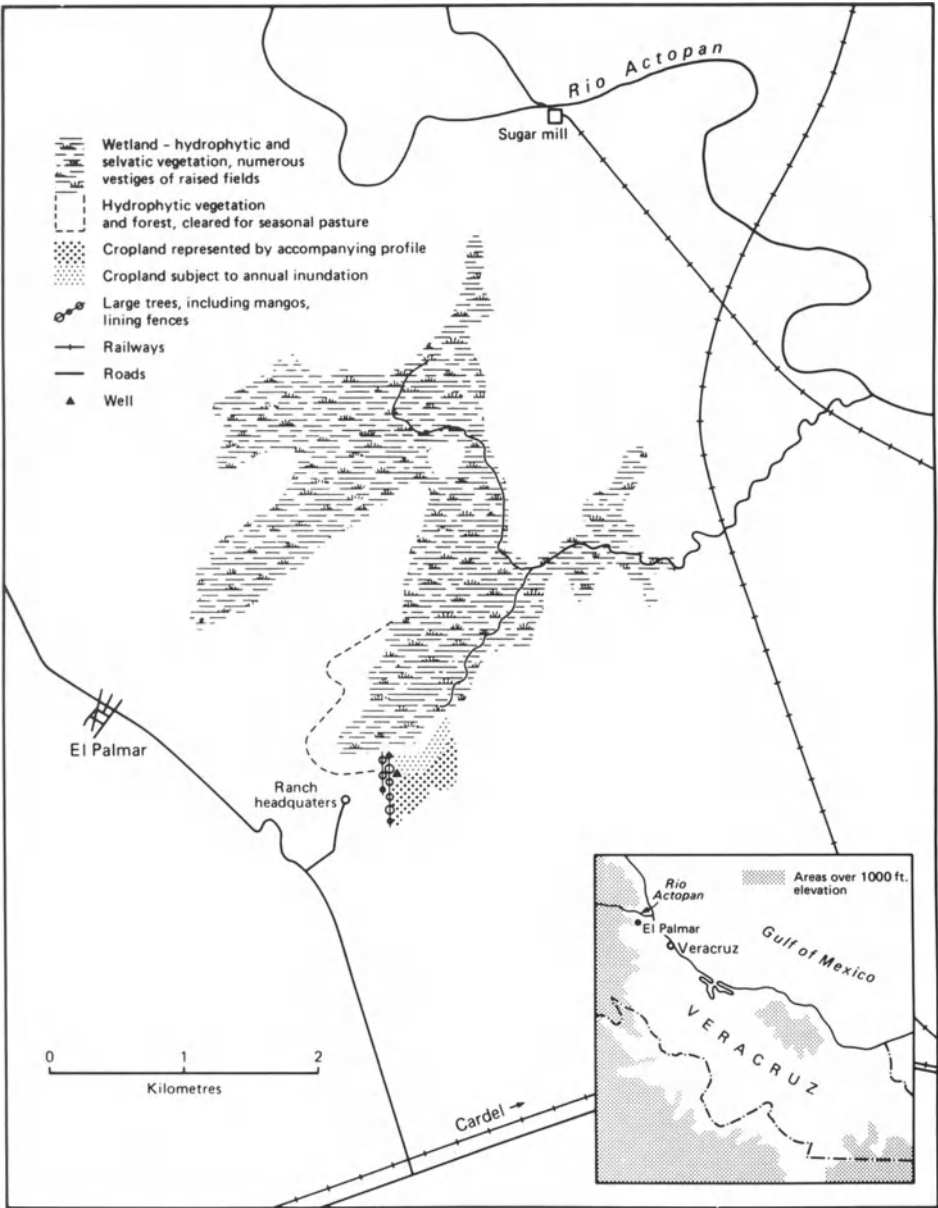


Figure 15.2. Locational map, El Palmar, Vera Cruz.

natural environment and in agricultural activities, as well as various related subjects.

15.2 The Environment

An outline of the usual form and location of the central Veracruz wetlands puts the agriculture of El Palmar into context. Three main elements of Gulf lowland physiography are especially important. From Jalapa or Huatusco, the lowland terrain slopes are deeply incised by west to east trending river valleys and reduced on the eastern periphery to numerous, low, rolling hills. The coast is fringed by generations of dunes, looping southward in conformity with the strong northerly winds that accompany the typical winter storms. They impede eastward drainage in many places. Alluvium laid down by the contemporary west to east flowing streams has subdivided the low belt between the extremities of the sloping terrain and the dunes. The result has been a scattering of shallow basins that are in effect backswamps.

The wetland of El Palmar is just such a basin. The alluvium of the Rio Actopan to the north impounds the runoff from the hills to the southwest into a bilobate area of swampland (Figure 15.2). This in turn is drained northeastward by a small, intermittent stream into the Rio Actopan.

The main west to east flowing streams throughout central Veracruz seem placid and unimpressive between their high banks in the dry season, but they quickly rise soon after the onset of the rains. The mean annual fluctuation measured at various stations along the Actopan, Antigua, and Cotaxtla rivers is from 3 to 5 m (Secretaria de Recursos Hidraulicos, 1971). The figures for one such station are recorded in Table 15.1. These fluctuations reflect seasonal variations in precipitation within catchment basins that include extensively settled mountainous terrain under a pronounced wet and dry climatic regime.

The intermittent streams draining the wetlands, sometimes referred to as arroyos, are sluggish and ill defined; they enter the larger streams just before these exit through the belt of dunes. The seasonal fluctuations of their water levels is less than one-half of that occurring in the channels of the nearby through-flowing streams. Their regime has not been systematically recorded, but estimates obtained from people living near wetlands in four separate drainage systems indicate a common seasonal fluctuation of approximately 2 m. This rhythm is of key importance to cattlemen in the region today; they must move their herds up- and downslope in response to it. Those agriculturalists with access to the margins of the backswamps advance downslope with their crops during the dry season and retreat before the floodwaters that come up with the rains.

Table 15.1. Annual maxima, minima, and fluctuation of the level of the Actopan River at El Naranjillo station, near the river's mouth.

	Water level (m)								
	1961	1962	1963	1964	1965	1966	1967	1968	1969
Max	6.96	4.75	5.50	2.90	4.36	6.50	3.72	3.16	5.00
Min	1.19	1.52	1.53	1.50	1.51	1.49	1.44	1.42	1.40
Fluctuation	5.77	3.23	3.97	1.40	2.85	5.01	2.28	1.74	3.60
Mean fluctuation	3.32								

Source: Secretaría de Recursos Hidráulicos (1971).

This same periodicity would have been critical to the pre-Hispanic agriculturalists of the region.

Average annual precipitation is lower over the lowlands behind Veracruz than it is over most of the rest of the Mexican Gulf lowlands. It drops from about 1500 mm near the coast to just below 1000 mm between Pase de Ovejas and Cerro Gordo and then goes up again to 2000 mm around Jalapa (Figure 15.1). The volcanic mountains of the Tuxtla region to the east and the spur of the Sierra Madre Oriental that arcs toward the ocean to the north impede moisture-bearing air masses in summer and winter, respectively. The 1000 mm of precipitation in this subhumid enclave falls mainly between late May and early November and sustains only a low tropical forest (*bosque tropical caducifolia*), now much altered by humans. Most species are leafless through the long dry season from November to May, giving the landscape a grey, desolate appearance relieved here and there by flowering trees.

The natural vegetation becomes generally more luxuriant as one goes from the subhumid zone towards the coast. The wetlands proper support high tropical rain forest (*bosque tropical perenifolia*), seen now only in scattered remnants, as well as aquatic communities (Rzedowski, 1978). It seems reasonable therefore to delineate a band of humid lowlands for broad reference purposes (Figure 15.1). In fact, the terrain between the extremities of the slopes and the dunes is a complex patchwork, within which the luxuriant wetland and dryer, slightly higher land are often juxtaposed. This is particularly striking in the dry season, when the wetlands proper are valuable reservoirs of moisture, taking on the aspect of oases.

15.3 The Community and its Agriculture

The families of El Palmar are members of an *ejido*, the characteristic group holding that emerged from the Mexican Agrarian Reform. Lands were expropriated from large land holdings and granted to landless agricultural laborers of the region and in-migrants. The older members of the community remember the conflict that this generated. At the present time, there are some sixty-five families in the ejido; together they hold 450 ha of land, 150 of which are located on what they aptly describe as the *orilla*, the margin of the wetland. This same margin is also sometimes called *bajío*, a term used widely in Latin America to indicate low-lying land subject to inundation (Santamaria, 1978). The *ejidatarios* have the right to use this land, but not to rent it or sell it. Each family has been assigned about 7 ha; of these 2 to 3 ha are on the orilla.

The 4 to 5 ha of hill land are used mainly for the wet-season cultivation of corn, the staple. This crop is known as the *temporál*. Some of this land, aggregated into communal parcels, is used for special crops like

sugarcane and papaya, or for pasture. These ventures have been stimulated by governmental cooperative credit. All of this is of less interest here than the rarer activities this community carries out on the wetland margin.

The orilla is shown schematically on the accompanying profile—as it was found in February of 1981 (Figure 15.3). The main rhythm of this landscape is the rise and fall of its water level; the difference is usually in the vicinity of 2 m. It rises early in the wet season, inundating the orilla from sometime in June to perhaps mid-September. Around the turn of the year, the inundated land is dry enough for agriculture. By February, the groundwater level is nearing its lowest levels, descending during the dry season only some 20 to 30 cm more. Available data on the behavior of water in this and other wetlands of central Veracruz have been obtained by field interviews and limited first-hand observation. More extensive field inquiry and a program of measurement is planned. A great deal remains to be learned.

During the year, the tropical deciduous forest on the surrounding hill lands goes from the lush green of the wet season to the grey and dismal dormancy of the dry season, relieved here and there by flowering trees. The tree growth that, together with hydrophytic communities, covers a good deal of the wetland proper is tropical high forest or its successional species; the foliage is luxuriantly green all year.

During the wet season, the ejidatarios carry out the *temporal* phase of the agricultural year. By February, remains of harvested corn can be seen upslope from the newly seeded plots of the land subject to inundation. During the wet season, the cattle use the hill land for pasture. By February, they have been brought down to feed on the natural vegetation in the wetlands, below the last of the cultivated fields, or they have been taken into small plots of cultivated fodder interspersed among the other crops.

Some of the dry-season crops of the orilla are started on a raised bed known as a *plantél*, similar to the *almácigo* of the chinampa system. The use of the *plantél* has been reported elsewhere in Veracruz and is considered to have a long tradition in the region (Kelley and Palerm, 1952.) Cane grass has already been seeded on the northern field peripheries to shield against the *nortes*, which accompany the frequent southward-moving storms during the dry season. The fields are sometimes ridged, and the plants set in furrows, in order to be as favorably located vis-a-vis residual moisture as possible and also to facilitate irrigation. Clearly, the microtopography is being manipulated to maximize the potential of this humid, fertile soil.

The crops on the orilla include annuals, such as tomatoes, chiles, watermelons, and melons, as well as the staples beans and maize. Together, this dry-season phase of the agricultural calendar is referred to as *tonalmil*. Papayas may be grown for two-year periods. If the *papayál* is not planted too far down the slope, if drainage is facilitated by furrowing between

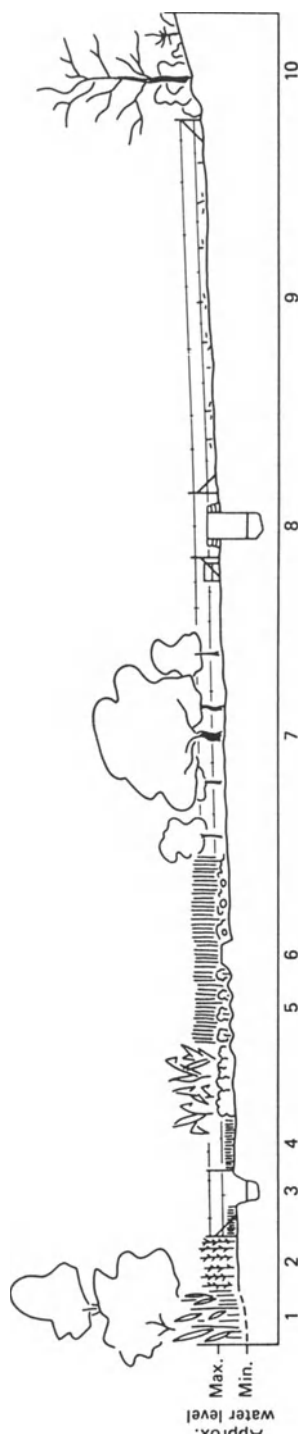


Figure 15.3. Schematic profile of the orilla. 1. Edge of the swamp, known locally as Aquachal or cienega, contains high forest species and hydrophytes intermixed (*Acrostichum aureum*, *Brosimum alicastrum*, *Canina iodica*, *Equisetum giganteum*, *Pontederia sagittata*, *Salix humboldtiana*, *Thalia geniculata*, *Typha augustifolia*).

2. Baldest of the dry season milpas.
3. Intake for the motorized irrigation system and water source for cattle.
4. Introduced pasture grasses.
5. A range of crops in the zone of inundation, known as *bajío* or *orilla*.
6. *Plantel*, or raised starting bed.
7. Fruit trees: *mango* along the fences; a grove of *limón* near upper margins of the *bajío*.
8. A lined well, enclosed in its own fence, with movable water tank.
9. Wet season milpa and pasture.
10. Selva baja caducifolia, known commonly as monte: (*Acacia farneciana*, *Acacia machrantle*, *Bursera simaruba*, *Cassia biflora*, *Cassia emareinata*, *Cochlospermum vitifolium*, *Croton niveus*, *Erythrina herbacea*, *Guazuma ulmifolia*, *Solanum tridynamum*, *Tabebuia chrysantha*, *Zanthoxylum fagara*).

the rows of plants (an antecedent of canalization), and if the inundation lasts for only a few days, this normally very water-sensitive plant is evidently not harmed. A grove of lime trees has been planted on the upper part of the inundated zone. The odd mango tree grows along the fences. The yields of the orilla are largely consumed in the home; small surpluses may be sold to itinerant buyers.

The entire orilla is intricately fenced. The land is subdivided among a good number of families. Also, cattle must be moved through the orilla from the wet-season pastures on the surrounding hills, down through a succession of harvested fields or planted pastures in the orilla proper during the dry season, to the lowest lands, beyond the most daring milpas, toward the end of the dry season.

A stone-lined well is found at a point along the slope that experience in the area has probably taught the local inhabitants is just above the usual limits of flooding. The water level in it was 2.65 m below ground level on May 21, 1981. The well is located along an east to west fence that roughly parallels the flood margin and is further enclosed in its own triangular fence. The bottom half of an oil drum that serves as a watering tank can be placed just upslope from the well and filled for cattle pastured there during the wet season and just downslope during the dry season.

The ejidatarios had aspirations for this land, of which more will be said below. From the ejidal officials, one gained the impression that the use they were making of it at the time was being deprecated as merely traditional, to be replaced by more mechanized, commercial exploitation as soon as possible. Recent developments at El Palmar are under investigation, as has been pointed out, but it is apparent already that this shift is underway. The photograph in Figure 15.4 was taken over the orilla in June of 1983. The view is opposite to that in Figure 15.5, southward rather than northward. The contrast between private ranchland and ejidal cropland is very clear. In the latter, the low-lying land that in 1980 was occupied by *tonalmil* has been allowed to revert to scrub; the slightly higher land is mostly being worked by machines in aid of commercial agriculture or ranching.

15.4 Dry-Season Agriculture Elsewhere in Mesoamerica

Comparative information on dry-season agriculture in the tropical lowlands of Mesoamerica enhances the understanding of what is being done on the margins of the wetland near El Palmar. Both examples of the cultivation of wetland/terra firma boundary zones and levee backslopes will be drawn in; the latter seem to have received the most extensive treatment. (Eventually, it may prove necessary to make detailed, systematic edaphic distinctions.)

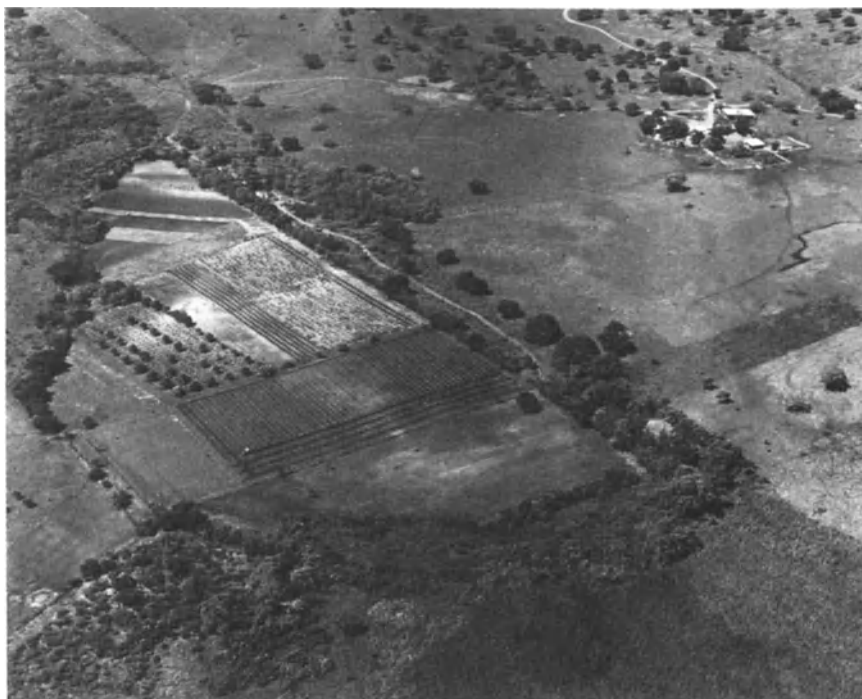


Figure 15.4. Aerial photograph of the *orilla* at El Palmar, June 1983.

The data are mostly scattered, scanty, and often given in a by-the-way fashion (e.g., Kelley and Palerm, 1952; Reina, 1967; Carter 1969; Drucker and Heizer, 1969; Reina and Hill, 1980). As Wilk (1981) has observed, many investigators, noting the relatively low yields of such agriculture, have considered it of minor importance. As he also notes, there are others who are beginning to appreciate the role of this activity in the evolution of agriculture in the tropics.

Coe and Diehl (1980) have described in some detail the dry-season agriculture that occurs in the floodplains of the Coatzacoalcos River. The Coatzacoalcos series soils of the levees are planted between November and February with a crop known in the region as *tapachol*; harvest comes in May or June. Some low-lying soils are planted even later, in March, with a particularly risky crop known as *chamil*. The authors argue that the environs of the Coatzacoalcos could have supported more people than it did during Olmec times and that the most productive agriculture of the region then was the dry season cultivation of levee soils, indeed that this, "is the most important clue to the rise of Olmec civilization at San Lorenzo Tenochitlán." (Coe and Diehl, 1980).

A crop known as the *marceño* is sometimes planted in Tabasco (Orozco-Segovia and Gliessman, 1979). This requires a rather audacious



Figure 15.5. Aerial photograph of the *orilla* looking southward.

foray into the lowest sections of the floodplain, where the water table may go down to some centimeters below the surface during the height of the dry season. The planting is often attempted in February or March; with luck, a harvest can be taken before the fields are too deeply reflooded.

Dry-season cropping has been reported out of the Maya area. The author encountered an instance along the Candelaria River in Campeche. Several Belizean examples could be cited (Wright et al., 1959; Lambert et al., 1979). The most interesting observations on dry-season agriculture in the Maya region have been made by Wilk (1981). There, this cultivation is known as *matahambre*, the hunger killer, or by its Mayan name *sak'ecuaj*, which evidently translates into sun field. Tonamíl, or its variants tonalmíl and tornamíl, has similar roots, coming from the Aztec *tonatl-el sol* and *milli-milpa* (Santamaria, 1978). It is carried out in those portions of the levee slopes that are judged neither too wet nor too dry. This is a gamble; a short dry season will mean the corn gets flooded out in a field too far downslope, a long dry season will mean desiccation in a field too far in the other direction. The best strategy seems to be to

spread a planting as much as possible along the topographic profile to ensure at least some yield.

Many aspects of dry season cultivation are similar to that of the wet season, but others differ. The vegetation on the levee slopes, usually a low-succession community called *sajál*, is mulched, not burned. The resulting field can be used for about 5 years in succession and needs to be fallowed only when the soil texture has become compacted by the sun, direct rainfall, and leaching. During these 5 years, it is reported, communities of insect, bird, and mammal pests have time to develop. Just how this would happen with annual flooding is not clear. The planting normally begins in mid-November, before the rainy season is over, and continues in stages until the rains appear to be slacking off. The harvesting is therefore also staggered. With luck, this means that a household will have a steady supply of green and dry corn for 4 or 5 months. The yields per hectare are usually lower and more variable (largely because of the pests) than those of wet-season agriculture, but their timing is highly advantageous. They may constitute a critical supplement to the yields of a meager previous wet-season crop or allow the household to leave stored reserves from that previous crop untouched. Moreover, there is little else to occupy the farmer during the dry season. This cultivation, then, is an important complement to the wet-season mainstay, and is flexible in several respects.

There is some cultural discordance to be considered when these various instances of dry-season cultivation by people rooted in lowland traditions are compared with that practiced by first or even second generation immigrants, such as the people of El Palmar. They may resort temporarily to learned or rediscovered lowland subsistence expedients, but seem more inclined than indigenous peasants to shift from them toward monoculture or ranching once that is possible.

All farmers are gamblers; in the various instances of dry-season agriculture described, the lowland *campesino* shows himself to be just that. But quite in line with his modest circumstances and the attitudes usually associated with peasantry, he is also a wary gambler, hedging his bets. At least one of the terms used to designate a dry-season crop, *tapachol*, the term Coe and Diehl (1980) report in common use along the Coatzacoalcas, has this sporting element imbedded. Santamaria defines it as *milpa venturera* (Santamaria, 1978). The actual risks, wherever this agriculture is carried out, lie mainly in the variability of the lowland rainfall of upland catchment basins. The floodplains or lake margins may dry out too late in the year, or too thoroughly in a prolonged dry season. Each reflooding may catch the crops still immature. Then there are the usual insect, bird, and mammal pests, worse evidently in this context than in wet-season agriculture on neighboring terra firma. Throughout Mesoamerica, there is the problem of northerly winds during the winter months. This is particularly serious right around the Gulf and is guarded

against at El Palmar by hedges of cane grass. The problem is how to reduce the risks. One can start the plants on a plantel, as at El Palmar, or wrap the seeds in leaves to germinate them before planting (West et al., 1969), all in order to reduce field time. A succession of crops can be planted on the emerging land, each attuned to a particular range in groundwater level. One can pump or lift water out of wells or water holes to irrigate at critical times and plant windbreaks of cane grass. With sufficient impetus, one could take more fundamental measures.

15.5 Postulations Regarding Pre-Hispanic Intensification

Given an increase in population in pre-Hispanic lowland communities or other factors that would increase the demand for the production of food crops, such as the need to render tribute, or an opportunity to dispose of surpluses profitably in neighboring regions, it is not difficult to envisage how dry-season agriculture on wetland margins would become urgent. The resulting initiatives need not have been associated with central political control, at least not in their early stages. The many discrete raised-field complexes of limited area in central Veracruz, as in the Maya lowlands or in the Huasteca, suggest the feasibility of incursions into swampland by individual communities. The agricultural potential of swampland may well have been suggested to those who lived around it by the swamp itself. It fills itself in naturally by means of sedimentation and plant growth; irregularly shaped hummocks gradually enlarge. This could be imitated or enhanced by spadework. In any case, there were considerable trans-Mesoamerican contacts at least as early as the Protoclassic Period, i.e., A.D. 1 to 300 (Grove, 1981). There are indications that the raised-field complexes of Central Veracruz date no further than that (Siemens et al., 1988). The knowledge of techniques of wetland agricultural intensification will probably have been widely diffused by the time of their inception.

The pattern of initial canalization is suggested by the perimeter of the raised-field complex near El Palmar and many of the others easily visible in the wetlands of central Veracruz on vertical air coverage or during air reconnaissance. The perimeters often appear raked in a downslope direction. Such a canal pattern will have greatly accelerated the yearly drying of the wetland margin and allowed access earlier than would otherwise be feasible. The resulting long, narrow planting platforms are open to terra firma on the upslope end and cut by transverse canals on the opposite end. A similar pattern has been noticed on the gentle backslopes of levees in a number of northern Veracruz floodplains (Siemens, 1982). However, the peripheral canals do not always tend directly downslope. The orientational scheme that pervades the raised-field complexes of the region has often led to canals that are diagonal to the slope (Sie-

mens, 1983). This seems very much like the topographic absurdities in roads and field boundaries in many hilly regions of western North America resulting from the imposition of the grid system.

Measurements of the elevation above sea level of the remains of fields along a transect across one complex near the village of El Pando in central Veracruz indicate a difference of at least 0.5 m between the surfaces of bordering fields and those in the lowest parts of the wetland. Unless there was uneven weathering after abandonment and truly massive build-up throughout the complex, we are dealing at El Pando with fields that paralleled in their surfaces the saucerlike basin in which they were built. It is quite likely that they were accessible only seasonally, but for various lengths of time, depending on where they were along the gentle slope of the saucer. Yearly flooding in this context need not have been destructive; on the contrary, it is likely to have added nutrients and helped control pests and weeds—in effect like a short fallow period.

As the dry season progressed in any given year, agriculture could progress from the raked borders further and further downslope, from the fields corresponding, perhaps, to those that have been called “border fields” in northern Belize to those called “island fields” (Turner and Harrison, 1983). The storage irrigation and fertilization function of the canals would have become progressively more important. In addition, the canals would have continued to facilitate access by boat and protected the fully surrounded fields from terrestrial insects and herbivores. The effectiveness of the whole system toward the end of the dry season is likely to have been enhanced by control of the outflow from main collector canals through simple damming.

The relationships between these components in the yearly round of agricultural activities would have depended on the levels to which it was possible to build up the surface of the fields and the degree of control, if any, that could be achieved over outflowing streams. These factors in turn would have been dependent on demographic and other pressures toward intensification. In any case, one can easily see in wetland agriculture a very useful complement to wet-season agriculture on terra firma. Food crops in quantity would be coming in at intervals all year.

The use of canalization to intensify the seasonal use of wetland margins has been suggested recently by other investigators. Wilk (1981) envisages it as a possibility in the sak'ecuaj fields of the Kekchi Maya, “Simple canals or ditches cut through the floodplain could drain moisture in wet years and reap rainfall in dry ones, thereby increasing the reliability of the crop.” Such canalization, he notes as well, could be analogous to terracing hillsides in order to trap dry-season moisture, which he judges would require more labor, and would seem to parallel the findings to date from aerial reconnaissance throughout the humid lowlands of central and northern Veracruz. Wherever the Totonaca or the Huasteca had access to wetlands, they used them; where these were not available, as

in the hilly terrain between the lower Tecolutla and Tuxpan, they resorted to terracing instead.

The wetland intensification that led to the full-blown chinampa system in central Mexico has recently been envisaged in considerable detail by Robertson (1983), in terms very similar to those used in the foregoing. The system is traced, as it is likely to have developed, from fugitive, marceñolike cultivation of seasonally exposed lakeshore, to extensive complexes of canals and planting platforms, enclosed by dikes. In the latter, water levels did not fluctuate more than a few tens of centimeters. This was full-blown chinampa agriculture with the whole series of intricate procedures that one commonly associated with the system. Such a reconstruction might well be taken into consideration in the ongoing archaeological investigation of the origins of the chinampa.

15.6 Current Analogues

The ejidatarios of El Palmar, as represented by ejidal authorities in 1981, aspired to various aspects of contemporary intensification. They envisaged the commercial production of sugarcane on the wetland margin they were then using for various subsistence crops. They claimed this had already been done on the colonial hacienda of the Lara family, from whom they obtained their land during agrarian reform. A preliminary examination of 1916 and 1922 cadastral maps obtained by Alba González Jácome indicates that they may well be right. Their postreform reversion to subsistence cropping would thus seem to represent a recent example of disintensification, probably one of many occurring at that time. To undertake the cultivation of sugarcane, the community needed to gain access to more of the wetland than they were using in 1981, but this was clouded by disputes over rights to unoccupied portions of it. They would need to drain this land and this would need financial help, as well as the cooperation of the federal governmental agency responsible for hydraulic works of this kind (*Secretaría de Agricultura y Recursos Hidráulicos*). These are the recent forces pushing for intensification. In pre-Hispanic times, it might have been imperatives generated by the growth of population in the region, as is generally accepted, or it might have been the necessity of coming up with tribute for the representatives of Central American rulers. In 1981, there was a joker in the deck, a vague plan for a new freeway running westward from the coast through the lands of the orilla.

In the meantime, the intensification of ranching has long been underway in virtually all of the wetlands of central Veracruz. The entire region has been used for ranching since the earliest years of the colonial period. Until late in the nineteenth century, however, this was an extensive, rudimentary pursuit. Cattle were often left to run wild and then

hunted for their hides and tallow. By the ranchers' design or the cattle's own adaptation, a kind of transhumance took place between wetland and terra firma. In the early twentieth century, and the detailed history of this remains to be traced, ranchers were clearing and draining some of the larger wetlands. These practices have expanded in recent decades. The objectives are to improve the forage of wetland pastures and to lengthen the yearly period of access to them.

By the time of our first inquiries at El Palmar in 1981, a further impetus toward land use change had been introduced into the picture—federal and state governmental promotion of the use of humid lands for cereal production in the context of the program known as Sistema Alimentario Mexicano (SAM). This is only one of the recent examples of governmental intervention in twentieth century rural land use in Mexico. SAM, even more than the need for fresh meat, reflected the production imperatives emanating from contemporary urban areas. It involved canalization for drainage and irrigation by means of pumps and tubing. Many of the newly cultivated lands probably have reverted to pasture since then.

15.7 Summary

The investigation of the form, function, and chronology of the most striking features of pre-Hispanic wetland intensification, the vestiges of canals and planting platforms that pattern many wetlands in the Mesoamerica lowlands, have proved an absorbing and productive inquiry—with a good deal more to come, no doubt. To fully appreciate the significance of these features, it is important to link them, at least hypothetically, with what is known or suspected regarding the microaltitudinal and seasonal interrelationships in tropical lowland agricultural activities during pre-Hispanic, colonial, and modern times. Complementarity in cropping on various types of land seems indicated in the lowlands since agriculture began, as well as pulses in the intensity of wetland use, and that of terra firma too. The raised field probably represented an epitome, as does mechanized cultivation of wetlands with full drainage and irrigation facilities. A seasonal use of the orilla, as carried out or at least remembered by the campesinos of El Palmar represents less intensive agriculture. The specific manifestation at any given time may vary greatly, but the interrelationships and the process are long-term phenomena. The understanding of them seems to be enhanced by the manipulation of analogues.

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16. Agricultural Systems of the Northeastern Hill Region of India

P.S. Ramakrishnan

16.1 Introduction

Agriculture is the predominant activity of a large majority of the world population. Industrialization of agriculture through large fuel energy subsidies, sophisticated chemical control of pests and diseases, and high-yielding crop varieties has resulted in huge increases in agricultural yields during the last half century. Such agricultural systems are efficient in terms of human time and labor but suffer from many deficiencies. They are highly inefficient from an overall energetic point of view, because five to ten units of fuel energy are required to produce a single unit of food energy (Steinhart and Steinhart, 1974). Apart from the ecological instability of the monoculture of a single high-yielding crop variety, industrialized agriculture also causes varied environmental problems related to the intensive use of fossil-based chemicals. The obvious inapplicability of such systems as models for development in an energy-limited world has led to renewed scientific interest in traditional systems of agriculture, which presumably offer ecological efficiency. In particular, shifting or swidden systems of cultivation have been held up as models of productive efficiencies where five to fifty units of food energy are obtained for each unit of energy expended (Rappaport, 1971; Steinhart and Steinhart, 1974). The possibility for increased crop production has been suggested (Greenland, 1975; Revelle, 1976; Mutsaers et al., 1981), without departing too much from the traditional system of shifting agriculture that has been

considered as the most evolved system for the forested areas of the tropics and subtropics (Nye and Greenland, 1960; Walters, 1971).

The present chapter considers the various land-use practices of the northeastern hill region of India. The predominant preindustrial agriculture systems, such as shifting agriculture, which involves slash and burn of the vegetation followed by cropping (known locally as jhum) and the valley agroecosystem on suitable flat lands between hill slopes, are contrasted with the semi-industrialized terrace agroecosystem that has been introduced recently as an alternative to jhum. The structural organization of the agroecosystems, economic yield, and energy efficiencies have been compared, and the ecological impact analysis of these three land use practices has been made in terms of hydrology and soil fertility. The functioning of a village ecosystem under jhum has also been considered to assess the ecological efficiencies of the various subsystems. The current landuse practices in the region have been evaluated for their stability and their interactions with other agricultural and food production systems.

16.2 Land-Use Pattern

Jhum is the chief land-use practice in the northeast hill region. The fallow period between cultivations of the same site, one jhum cycle, is often short, ranging up to 4 or 5 years. But prior to recent times, when the population pressure was not heavy, and land availability did not limit the cycle, it was a long one of 20 to 30 years (Ramakrishnan and Toky, 1978; Ramakrishnan, et al., 1981a). The average size of a jhum plot varies from 1.0 to 2.5 ha. The average family consists of two adults and three to four children.

16.2.1 Low Elevation Jhum

The low-elevation jhum prevalent at Burnihat (about 90 km north of Shillong at 26° N and 91° E) is typical of the version found throughout the northeastern hill areas in that (1) the cultivation is done on slopes of 20 to 40%; (2) the climate is monsoonic, with a high rainfall of over 2200 mm followed by a dry winter and a brief, warm summer supporting a mixed subtropical humid forest; (3) the normal jhum cycle is 4 to 5 years, but rarely may last for 10 to 30 years; and (4) more importantly, the forest is clear felled before cropping (Toky and Ramakrishnan, 1981a).

During the winter months (December to January), the undergrowth is slashed, and small trees and bamboos are felled. Short tree stumps and large tree boles are left intact. The underground organs of different species are not disturbed. This laborious process is often completed by the men from two or three families. Such a joint effort is one of the essential

ingredients of a well-knit social organization. This effort, along with the process of allotment of sites for jhum by the village headmen, helps to promote kinship among the members of the village community.

Towards the end of March or the beginning of April, before onset of the monsoon, the debris is burnt in situ. Before burning, a fire line is cleared around the field. Burning is often repeated to destroy any unburnt material that first has been collected in heaps. A bamboo hut is built for temporary living. The family's presence protects the field from wild animals.

Sowing is done after the first few monsoon showers. The seed mixtures used for different jhum cycles may vary considerably. Whereas cereals are emphasized under long jhum cycles, perennials and tuberous crops are emphasized under short jhum cycles. The details of crops sown are given in Table 16.1. Some eight to thirteen crops are grown together at Burnihat, but up to thirty-five species may be planted elsewhere in the Garo and Naga hills (Kushwaha, 1981). Seeds of pulses, cucurbits, vegetables, and cereals are mixed with dry soil from the sites to ensure their uniform distribution, and broadcast soon after the burn. Maize seeds are dibbled at regular intervals amongst other crops. Similarly, rice is sown into the crop mixture by dibbling with a long stick after the first rainfall in mid-April. Semiperennial and perennial crops, such as ginger, colocasia, tapioca, banana, and castor are sown intermittently and at random throughout the growing season. The leaves of *Ricinus communis* are used for rearing young silkworm caterpillars. The leaves of some dicot trees also may be used for this purpose or for feeding older caterpillars. Crops are harvested as they mature, making more room for the other crops left behind. After clearing and burning, the land is used for only 1 year, except when maintaining perennial crops of banana, pineapple, or orange.

Throughout the cropping period, weeds pose a problem. The most common weeds are root sprouts, rhizome sprouts, stump sprouts, tree seedlings, grasses, and herbs. Under long jhum cycles, the problem is less severe than under short jhum cycles, where many weeds, particularly *Imperata cylindrica*, keep sprouting from underground rhizomes and are difficult to eradicate. Others, like *Eupatorium odoratum* are kept under control through frequent slashing. Hand hoeing is usually done twice (3 to 4 times under short cycles) during the cropping, mainly by women.

16.2.2 High Elevation Jhum

The jhum at higher elevations in Meghalaya is a modified version of the typical one outlined above. It is commonly practiced around Shillong (Mishra and Ramakrishnan, 1981). The vegetation there consists of sparsely distributed pine trees (*Pinus kesiya*) with much undergrowth of shrubs and herbs. The pine trees are not felled, but the lower branches are slashed in December. The slash is arranged in parallel rows running

Table 16.1. Economic yield of crops under 30-, 10- and 5-year jhum cycles and terrace agroecosystems at lower elevations

	Dry weight yield (kg/ha/yr)			Terrace
	Jhum cycles			
	30-yr	10-yr	5-yr	
Grain and seed				
<i>Oryza sativa</i>	1,161	378	66	955
<i>Sesamum indicum</i>	448	541	25	21
<i>Zea mays</i>	770	397	30	144
<i>Setaria italica</i>	193	23	9	ND
<i>Phaseolus mungo</i>	10	ND ^a	ND	7
<i>Ricinus communis</i>	5	ND	ND	8
Total	2,585	1,339	130	1,135
Leaf and fruit vegetables				
<i>Hibiscus sabdariffa</i>	44	139	96	91
<i>Hibiscus esculentus</i>	ND	50	ND	ND
<i>Capsicum frutescence</i>	ND	1	ND	ND
<i>Lagenaria leucantha</i>	140	81	ND	ND
<i>Cucurbita maxima</i>	62	ND	ND	95
<i>Cucumis sativa</i>	16	ND	ND	ND
<i>Momordica charantia</i>	ND	5	ND	10
<i>Phaseolus vulgaris</i>	ND	ND	ND	15
<i>Musa sapientum</i>	ND	105	488	180
Total	262	381	584	391
Tuber and rhizome				
<i>Manihot esculenta</i>	339	1,352	690	1,308
<i>Colocasia antiochorum</i>	260	294	180	90
<i>Zingiber officinalis</i>	10	ND	ND	22
<i>Curcuma longa</i>	ND	ND	ND	16
Total	609	1,646	870	1,436
Silk worm				
Cocoon (silk)	4.0	ND	ND	4.0
Pupae (without cocoon)	0.2	ND	ND	0.2
Total	4.2			4.2

Source: Toky and Ramakrishnan, 1981a.

^aND = no data; crop was not grown in this system.

down the slope and then allowed to dry. In the month of March, soil is placed on top of the slash, so as to form ridges alternating with furrows of compacted soil running along the slope. Consequently, the burn of the slash is slow and controlled. A fire line of cleared vegetation around the field helps to check its spread.

The crop mixtures differ from that of the low elevation jhum in that tuber crops, such as *Solanum tuberosum*, *Ipomoea batatas*, and *Colocasia antiquorum*, are planted on the ridges. These are planted soon after the burn and before the onset of the monsoon. Sowing of *Zea mays*, *Phaseolus vulgaris*, and a few cucurbits are done just after the onset of the monsoon. Along each ridge, potato and *Zea mays* are sown together in three distinct

Table 16.2. Economic yield of crops under 15-, 10- and 5-year jhum cycles and terrace agroecosystems at high elevations

	Dry wt. yield (kg/ha/yr)			Terrace
	Jhum cycles			
	15-yr	10-yr	5-yr	
Grain and seed				
<i>Zea mays</i>	42	59	62	123
<i>Phaseolus vulgaris</i>	7	4	ND	ND
Total	49	63	62	
Leaf and fruit vegetables				
<i>Cucurbita maxima</i>	272	257	ND	ND
<i>Cucumis sativas</i>	9	6	ND	ND
<i>Brassica oleracea</i>	76	27	164	ND
<i>Colocasia antiquorum</i>	2	2	ND	ND
<i>Colocasia antiquorum</i> (stem)	0.4	0.4	ND	ND
<i>Cucurbita maxima</i>	3	3	ND	ND
<i>Cucurbita maxima</i> (flower)	0.4	0.5	ND	ND
Total	363.8	296.9	164	
Tuber				
<i>Ipomoea batatus</i>	1	1	ND	ND

Source: Mishra and Ramakrishnan, 1981.

ND = no data; crop was not grown in this system.

rows. *Colocasia antiquorum* is generally confined to the top and bottom part of each ridge, and the cucurbits are sown at random. *Phaseolus vulgaris* is sown around pine trees for their support.

After the harvest of the tuber crops in July and August, a winter crop of potato is sown along the ridges. Harvesting of *Zea mays* and the legume, *Phaseolus vulgaris*, is done in September and October, after which *Brassica oleracea* seedlings are planted along with the winter crop of *Solanum tuberosum*. The second potato crop is harvested during November, and then the field is left uncultivated between December and March. If a second year of cultivation is done, the same procedures are followed; otherwise the land is fallowed for natural regrowth of vegetation.

The mixture of crops used varies, depending on the jhum cycle (Table 16.2). Under a long jhum cycle of 15 years, cropping is done for 1 year only, and no fertilizer is used. Under a 10-year cycle, organic manure in the form of pig dung and vegetable manure is applied at the rate of 600 kg/ha/yr (oven dry weight). Under a 5-year jhum cycle, cropping is done for 2 to 3 years continuously after slash and burn, but the crops grown are only *Solanum tuberosum*, *Zea mays*, and *Brassica oleracea*. During cropping, both organic (pig dung and vegetable manure) and inorganic (nitrogen:phosphorus:potassium [NPK], 1:1:1) fertilizers are applied at the rate of 1000 kg/ha and 20 kg/ha, respectively, in the first year of cultivation and 1850 kg/ha and 20 kg/ha, respectively, in the second year.

Herbaceous weeds grow from seeds, rhizomes, or root sprouts. *Eupatorium adenophorum*, a noxious weed, may arise through seeds or root sprouts. *Imperata cylindrica* comes up chiefly through fire-resistant underground rhizomes and is common in the low-elevation jhum. *Pteridium aquilinum* and *Dicranopteris linearis* are other important weeds that, along with root or stem sprouts of trees and tree seedlings, are kept under control through frequent slashing. Hand hoeing along the ridges may be done 2 to 3 times during the season.

16.2.3 Valley Agroecosystem

Unlike jhum, valley agriculture is a monoculture of rice and is practiced throughout hill terrain, both at low and high elevations. It is a sedentary form of agriculture. Wet cultivation of rice (*Oryza sativa*) is a complementary system of land use, and is done wherever the terrain permits, on flat lands between hill slopes. The soil is fertile due to nutrient washout from the hill slopes, and does not need added fertilizer. The main advantage is that the land gives sustained yield year after year.

At lower elevations, two crops are planted annually on the same land. Field preparation for the first crop is done in February and March. Seedlings are raised in nursery beds in the month of March, transplanted at the beginning of April, and the crop is harvested by the end of July or early August. Immediately after the first harvest, the fields are again prepared, with harvesting completed by October and November. Subsequently, the land is fallowed between November and March.

At high elevations, the land is well prepared before sowing the seeds by broadcasting after the first few showers in June. Harvesting is done in November, after which the land is fallowed until the following May or June. Only one crop is raised per year.

In all of these areas, the operations of weeding, transplanting, harvesting, and threshing are done manually by both male and female members of the family. Only male members prepare the field. The average size of land under valley cultivation, for a family of 5 members consisting of two adults and three children, is 0.5 to 0.75 ha. Not more than 10 to 15% of the cultivated land area would be under this form of land use.

16.2.4 Terrace Agroecosystem

Recently, local governmental agencies attempted to provide bench-terraced land free to local farmers, as an alternative to jhum. But this is not a common form of land use, and this experimental attempt has failed to catch on. The cropping pattern on bench-terraced land is similar to jhum but needs a heavy input of organic and/or inorganic fertilizers. Initially, the governmental agencies provided free fertilizer but now the farmers bear the cost. Here cropping may be done for about 6 to 8 years on the same site. After this period, the site may be abandoned, partly because

of lower returns from poor soil fertility and increased weed problems and partly due to washout of soil from the peripheral areas of the terraces. This soil loss necessitates the continual repair of the terrace boundaries and reduces the effective land area for cropping. The average size of a terraced plot is 1 to 1.5 ha for an average family of five members consisting of two adults and three children.

16.3 Economic Yield of Agricultural Systems

16.3.1 Mixed Cropping and its Significance

Mixed cropping is very common in shifting agriculture throughout the world (Conklin, 1957; Nye and Greenland, 1960). This not only provides an all-purpose diet to the farmer but even meets some of his other needs, such as fiber and fuel wood. The crops may be planted simultaneously, as in the present case, or root crops may be planted after the harvest of cereals, as in the forest zones of Ghana (Nye and Greenland, 1960). In mixed cropping under low elevation jhum, several crop species with diverse growth habits develop a multistoried canopy with perennial crops, such as cassava, banana, and castor occupying the top layer, cereals forming the middle layer, and cucurbits and legumes forming the lowermost stratum. Thus an extraordinarily large leaf area index is possible. The multistoried canopy protects the land from excessive soil erosion and leaching once the crop cover is established. Multiple cropping provides an “insurance” policy to the cultivators because some crops are likely to give a good return even if there is partial or complete failure of other crops. Diverse root habits and mineral nutrient requirements enable optimum use of space and resources. The incidence of pests and diseases also is minimized under mixed cropping. The preplanting burn contributes to controlling harmful ants and other insect pests.

The successive harvesting of crops also confers some advantages. After harvesting maize and *Setaria italica*, rice gets more space at the peak of its growth period. Successive harvests of cereals create additional space for the remaining perennial crops, which also receive humus and nutrients from the decay of plant debris. In addition, a more even distribution of labor is ensured.

16.3.2 Low-Elevation Jhum

Although the economic yield from cereals is greater under a long jhum cycle (30-year), more semiperennial and perennial crops are planted under shorter cycles (10- and 5-year). Thus yields of, for example, *Manihot esculenta*, increase under shorter cycles (Table 16.1). Even the yield per plant for tuber and rhizomatous crops was higher under short jhum cycles of 10 and 5 years compared to a 30-year cycle (Toky and Ramakrishnan,

Table 16.3. Monetary budget under jhum, terrace, and valley agroecosystems^a

Low Elevation					
	Jhum			Terrace	Valley
	30-yr	10-yr	5-yr		
Input	2,616	1,830	896	2,542	4,843
Output	5,586	3,354	1,690	3,658	5,565
Net gain/loss	2,970	1,524	794	1,116	722
Output/Input	2.13	1.83	1.88	1.43	1.14
High Elevation					
	Jhum			Terrace	Valley
	15-yr	10-yr	5-yr		
Input	3,281	3,430	3,154	6,004	1,671
Output	19,790	14,171	8,188	12,561	3,161
Net gain/loss	16,509	10,741	5,034	6,557	1,490
Output/Input	6.03	4.13	2.60	2.09	1.89

^aAll values reported as rupees/ha/yr.

1981a), in spite of the shorter cycle's lower soil fertility (Ramakrishnan and Toky, 1981). Such higher yields may arise because rapid initial growth gives quick cover and also shades out weeds. Furthermore, deep and extensively branched root systems ensure efficient use of available nutrients. On the other hand, the yield per plant of grain and seed crops was markedly lower under shorter jhum cycles. The more efficient resource use of leafy perennial/tuber/rhizomatous crops would explain a shift towards them under short jhum cycles when soil fertility is very low (Ramakrishnan, unpublished).

As is to be expected, shortening the jhum cycle results in drastic reduction in overall economic return. This reduction is not obvious from Table 16.1, because the individual crop yields are not comparable and, therefore, do not indicate the total return. However, this becomes evident when the monetary return, calculated on the basis of prevailing market rates, is considered as in Table 16.3. This decrease in economic return under short jhum cycles is related to reduced soil fertility (Ramakrishnan and Toky, 1981) and increased weed interference (Kushwaha, et al., 1981; Mishra and Ramakrishnan, 1981). In Table 16.3, the monetary input for jhum is the cost of labor for slash and burn and for weeding (calculated on the basis of prevailing rates). However, this labor is free to the farmer because it is provided by the farmer's family. In spite of the decrease in the labor cost for slashing the vegetation under shorter jhum cycles, the output/input ratio declines.

16.3.3 High-Elevation Jhum

Though rice still forms the staple diet of the local tribe, the Khasis, potatoes have been widely cultivated since they were first introduced into

this region a few decades ago. As is seen from the yield data, potatoes and other rhizomatous crops have the greatest yield under jhum, followed by vegetable crops. As at low elevation, the yield declined drastically with the shortening of the jhum cycle (Tables 16.2 and 16.3).

A comparison of the monetary budget from jhum at low and high elevations (Table 16.3) leads to some interesting conclusions. The output from the low-elevation system, where rice and other seed and grain crops are emphasized, is very low compared to the high-elevation system. In spite of the high input for land preparation in the high elevation system, the output/input ratio is much higher than that for the low-elevation jhum. Further, as discussed earlier, the emphasis on potato and other tuber/rhizomatous crops gives better returns from the generally less fertile soil at high elevations (Mishra and Ramakrishnan, 1983a). Potatoes are mainly produced for export from the village ecosystem.

16.3.4 Valley Agroecosystem

The rice yield with two croppings at lower elevation is 3710 kg/ha/yr, whereas at higher elevation, the yield from a single crop is 2822 kg/ha/yr. Although the monetary output from this system at lower elevation is comparable to one of mixed cropping under a 30-year jhum cycle, the return from the high-elevation valley cultivation is very low compared to potato cultivation under all jhum cycles. The high monetary input for valley cultivation is due to the care and effort that goes into ploughing and other land preparations and the need for frequent weeding due to the washout of weed seeds from the hill slopes. However, settled valley cultivation is tenable in the northeastern hill region, both from an economic and an ecological point of view. The main advantage of this system lies in the raising of crops consistent in yield, year after year, from the same plot.

16.3.5 Terrace Agroecosystem

The yield here is low in relation to inputs of labor and fertilizer. The fertilizer input under terrace cropping is as much as 60 kg of N, 30 kg of P_2O_5 and 30 kg of K_2O , whereas at high elevation, it is even more, at 3000 kg of organic manure and 740 kg of NPK (1:1:1) per hectare per year. The relatively poor yield under terrace cultivation (Table 16.2), in spite of heavy input of fertilizers, is due to heavy losses of nutrients through leaching (Ramakrishnan, et al., 1981b; Toky and Ramakrishnan, 1981; Mishra and Ramakrishnan, 1983b).

The monetary output is comparable to that from a 10-year jhum cycle. However, the output/input ratio is lower (Table 16.3). The inefficiency of terrace cultivation would be magnified if the cost of terracing (not included here) were taken into account, along with the life of the terraces, which is not more than 6 to 8 years (Mishra and Ramakrishnan, 1981;

Toky and Ramakrishnan, 1981a). As under jhum, the monetary efficiency of this form of land use is higher for potato cultivation at higher elevations than cereal cropping at lower elevations.

16.4 Energy Budget of Agricultural Systems

Apart from economic yield of crops and monetary cost benefit analysis, energy budget analysis is one of the many ways to evaluate agricultural system efficiency. Fossil energy (fertilizer, fuel, etc.), land, and labor are the three important resources for modern agriculture. These three are related to one another and could compensate, at least in part, one for the other. In the northeastern hill areas of India, jhum, valley agriculture and terrace agriculture are basically labor intensive with an energy output/input ratio of 48 on one extreme and 7 on the other. However, these efficiencies are related to the land use pattern and environmental constraints.

16.4.1 Energy Efficiencies

The energy efficiency of land use patterns at both low and high elevations follow a similar trend, and therefore the discussion here is based on the former (Toky and Ramakrishnan, 1982). Jhum is still the chief land use in the hill regions of northeast India and elsewhere in the humid tropics. One reason is the high energy efficiency of the system associated with longer cycles. The only energy input into the system is manual labor, which is provided by the farmer. In a study on rural India, Revell (1976) estimated that over 50% of all hours worked are spent directly on agriculture. Our own studies on jhum (Mishra and Ramakrishnan, 1981; Toky and Ramakrishnan, 1982) suggest that under a mixed cropping system with successive harvests of crops, labor is uniformly distributed throughout the year. Men do the harder tasks, such as slash and burn of the vegetation and related land preparation, and women, along with men, do the lighter jobs, such as sowing of crops and weeding.

According to Rappaport (1971), the Tsembaga people of the New Guinea highlands obtained an average of 16 units of food energy for each unit of human energy input. Others have reported equally high or even higher efficiency values with output/input ratios of up to 54 (Lewis, 1951; Norman, 1978; Uhl and Murphy, 1981). Most of these studies, however, do not mention the length of the swidden cycle and its relationship to energy efficiency. Our studies on three jhum cycles of 30, 10, and 5 years at lower elevations suggest overall efficiency values ranging from about 34 to 48, depending upon the cycle (Table 16.4). This is understandable because: (1) the labor energy expended for clearing and burning under longer cycles (30- and 10-year) is greater than under the 5-year cycle

Table 16.4. Energy efficiencies of agricultural systems at lower elevations

Agricultural systems	Energy (MJ/ha/yr)		Output/Input
	Input	Output	
Jhum			
30-year cycle	1,665	56,766	34.1
10-year cycle	1,181	56,601	47.9
5-year cycle	510	23,858	46.7
Terrace	6,509	43,602	6.7
Valley (two crops)	2,843	50,596	17.8

Source: Toky and Ramakrishnan, 1982.

(woody vegetation of the longer cycles is harder to fell than the younger, more herbaceous vegetation); (2) energy expended for weeding increased with shortening of the jhum cycle (see the discussion below); and (3) considerable reduction in economic yield occurred with shortening of the jhum cycle, as shown above.

The valley agroecosystem has a fairly high output/input ratio of 17.8. But this ratio is lower than that for jhum due to lower energy output from a monoculture of rice compared with a mixture of crops under jhum and higher labor cost for land preparation and weeding. The efficiency of the terrace agroecosystem is very low due to heavy energy inputs for labor to prepare the terraces in the first year and maintain them in subsequent years and heavy fertilizer inputs. This system is comparable to other sedentary and more modern Indian agricultural systems, where nine units of food energy are harvested for each unit of fossil fuel energy put into the system (Mitchell, 1979), but better than most western agricultural systems, where the yield is one or two units of food energy per unit of energy input (Spedding, 1975; Leach, 1976; Spedding and Walsingham, 1976; Pimentel and Pimentel, 1979).

16.4.2 Energy in Relation to Land Use

The comparative energy efficiency (or for that matter, the monetary efficiency discussed earlier), cannot be considered in isolation, but needs to be discussed in relation to the land-use pattern. If not, the energy efficiency values for different jhum cycles could lead to distorted comparisons. At lower elevations, the effective energy output per hectare would decrease due to a correction factor of $\frac{1}{30}$, $\frac{1}{10}$, or $\frac{1}{5}$, so that an effective output of only 1892, 560, or 4771 MJ/ha is obtained. If land is not a limiting resource, then the greater solar energy input to a larger area of the jhum system could be used to offset imported energy and this would ensure harmony of the longer cycles with the environment, at the same time ensuring rational returns for the farmer. However, the land is in short supply due to increased population pressure and reduced

acreage available for jhum due to environmental degradation from arrested succession by weeds and desertification in extreme cases (Ramakrishnan, et al., 1981a, b). On this basis, a 10-year jhum cycle is the most efficient in terms of energy ratio and land use (Toky and Ramakrishnan, 1982), though valley and terrace cultivation have a much higher effective output, with 43602 MJ and 50596 MJ, respectively. Terrace cultivation is not a stable system because of the need for heavy input of fertilizers, the utilization efficiency of which is low, due to high infiltration losses (Toky and Ramakrishnan, 1981b; Mishra and Ramakrishnan, 1983b) and the consequent environmental problems (Ramakrishnan, 1980). In the ultimate analysis, this form of land use has not found much favor with the local population. From an overall efficiency of the system in terms of land use, valley cultivation of rice seems to be attractive.

16.4.3 Energy and Land Use at High Elevations

The broad generalizations about lower elevation agricultural systems discussed above also apply to the high-elevation systems (Mishra and Ramakrishnan, 1981), except for the following major differences in the energy budget:

1. The output/input ratios for jhum are generally lower (26, 10, and 5 for 15-, 10-, and 5-year jhum cycles, respectively) than at lower elevations, particularly under 5- and 10-year cycles, due to heavier labor input for preparation of the plot and organic/inorganic manure input into the system.
2. The terrace cultivation is also less efficient (output/input ratio of 1.7) due to heavier labor cost and increased fertilizer use.

Though jhum and terrace systems at higher elevations are less efficient from an energy angle, they undoubtedly are economically more profitable, as discussed in the preceding section.

16.5 Hydrology and Nutrient Losses From Agricultural Systems

After slash and burn, the system loses its ability to hold nutrients due to lack of plant cover, especially in the initial stages when crop/weed cover is not yet established. Nutrient loss is aggravated by damage to the physical structure of the soil and more frequent cropping under shorter jhum cycles. The following account considers the nutrient loss pattern from the soil under the low elevation jhum, by comparing jhum and terrace cultivation to the higher elevation agroecosystems.

16.5.1 Low Elevation Jhum

The dried slash under jhum is burned sometime in the months of March and April, a few weeks before the onset of the monsoon. This is a dry

Table 16.5. Nutrients released through ash and blowoff under three jhum cycles at lower elevations

Nutrients (kg/ha/yr)	30-yr		Jhum cycle 10-yr		5-yr	
	Release	Blowoff	Release	Blowoff	Release	Blowoff
P	313	147	262	156	151	43
K	1,739	817	2,070	1,229	262	156
Ca	956	449	193	115	116	33
Mg	209	98	152	90	114	32

Source: Toky and Ramakrishnan, 1981b.

period, with strong wind currents and therefore much nutrient loss occurs from a blowoff of ash (Table 16.5). The ash released under a 30-year jhum cycle had very high levels of calcium owing to the predominance of broadleaved trees. Under a 10-year cycle, the ash had larger quantities of potassium due to the predominance of a bamboo species, *Dendrocalamus hamiltonii*, which is a heavy accumulator of potassium (Toky and Ramakrishnan, 1981b). Although volatilization of nutrients also occurs during the burn (Nye and Greenland, 1960; Salas and Foster, 1976), it has not been quantified during this study.

A comparison of the hydrology of the jhum agroecosystems with 5- and 10-year fallow regrowth showed sizeable increases in runoff water and sediment loss during cropping (Table 16.6). The loss of sediment and water from runoff and percolation increased with the shortening of the jhum cycle. This may be related partly to poor physical characteristics of the soil and partly to poor crop cover (Toky and Ramakrishnan, 1981a). Because of the highly porous soil, percolation losses of water are often in excess of 50% of that lost through runoff. From a conservation viewpoint, this implies that percolation losses may still be heavy, even if erosion is checked through terracing, which is often advocated as an alternative to jhum. Much of the losses from the jhum systems occur in

Table 16.6. Hydrology and sediment loss from jhum systems and the fallows at lower elevations (after Toky and Ramakrishnan, 1981b)

Site	Run-off water (cm)	Percolation water (cm)	Sediment loss (t/ha/yr)
Agroecosystem			
5-year jhum cycle	37	23	30
10-year jhum cycle	34	19	23
30-year jhum cycle	29	14	23
Fallows			
5-year	27	21	1.1
10-year	19	14	0.8

Source: Toky and Ramakrishnan, 1981b.

the months of May and June when the crop cover is not yet established, and decline drastically in subsequent months (Toky and Ramakrishnan, 1981b).

The pattern of nutrient loss showed a similar trend. This was due to large volumes of surface water flow containing higher concentrations of nutrients, and the lack of crop cover mentioned above. Late in the season, actively growing crops and weeds reduce leaching and runoff losses by providing good soil cover and canopy interception. Furthermore, they conserve nutrients through rapid uptake. The loss of potassium from the agroecosystems was very heavy, particularly under a 10-year jhum cycle when *Dendrocalamus hamiltonii* was the chief slash material (Table 16.7). Even though the quantity of percolation losses of water from the agricultural systems and the fallow were similar, the quality was different. The amount of nutrients in percolation water of jhum cycles was much higher. Nitrate losses through percolation water are much heavier than through runoff.

In 1- and 5-year fallows, the loss of sediment and nutrients from the system was drastically reduced (Table 16.7). The biogeochemical recovery of the forest ecosystem depends upon the establishment of biotic regulation of ecosystem functions, such as uptake of nutrients and water, storage of nutrients in the biomass, and their gradual release through litterfall, and withstanding erosion through plant cover. Even the weedy cover of *Eupatorium*, *Imperata*, and others established during the first five years, as well as the larger species, such as bamboo and trees that come up later, help in the transfer of nutrients from the soil to the vegetation pool, and so reduce loss through runoff and percolation. More frequent cropping under a short cycle of 4 to 5 years contributes to the rapid depletion of soil fertility and the consequent loss of ability of the system to recover.

16.5.2 High-Elevation Jhum and Terrace Agroecosystem

Only the salient points of difference between high-elevation jhum and terrace cultivation have been presented. In a study of the high-elevation land use at Shillong, the hydrology and related nutrient losses from the modified version of jhum under two cycles of 10 and 5 years were compared and contrasted with terrace cultivation (Mishra and Ramakrishnan, 1983a). This situation is different in that: (1) the soil here is podsollic with higher acidity; (2) the regrowth of jhum fallows is less rapid due to lower temperatures, higher acidity of the soil and poor regeneration under pine litter; and (3) organic and inorganic fertilizers are used during both jhum and terrace cultivation.

For reasons related to poorer soil qualities and slower regrowth of fallows under jhum, the loss of sediment and nutrients, such as potassium, through runoff tend to be much higher compared to the loss from the

Table 16.7. Nutrient losses through runoff and percolation water at lower elevations

Element	Jhum cycle losses (kg/ha/yr)						Fallows losses (kg/ha/yr)					
	30-yr			10-yr			5-yr			5-yr		
	Runoff	Percolation		Runoff	Percolation		Runoff	Percolation		Runoff	Percolation	10-yr
PO ₄ -P	1.1	0.1		1.3	0.1		0.9	0.1		0.1	0.02	0.1
NO ₃ -N	3.7	8.8		4.2	10.6		5.3	9.2		0.8	1.10	0.5
K	64.7	15.1		91.2	21.2		51.0	13.7		0.9	0.50	1.7
Ca	15.1	5.3		15.9	4.9		13.8	4.6		2.0	2.70	1.1
Mg	6.3	2.5		5.4	2.1		9.5	2.3		1.3	0.90	0.8
												(1.60)
												0.50

Source: Toky and Ramakrishnan, 1981b.

Table 16.8. Sediment and potassium losses through runoff from agroecosystems of higher elevations

Material lost	System				
	Jhum cycles losses (kg/ha/yr)		Fallows losses (kg/ha/yr)		Terrace losses (kg/ha/yr)
	10-yr	5-yr	10-yr	5-yr	
Sediment	49.7	54.9	3.5	1.9	33.9
K	88.1	104.6	19.6	2.3	33.1

Source: Mishra and Ramakrishnam, 1983a.

low-elevation jhum (Table 16.8). This is in spite of the great effort put into land preparation. Otherwise, the loss patterns are similar to the low-elevation systems discussed above.

Sediment loss during cropping under terrace cultivation was markedly lower than under jhum. There was a 38% and 25% reduction in the first and second year of cropping, respectively, compared to that under a 5-year jhum cycle. However, sediment loss tends to increase in subsequent years of terrace cropping, as indicated above. The nitrogen and phosphorous losses from the terrace agroecosystem are often less than under a 5-year jhum cycle, although percolation losses of these nutrients are consistently higher (Mishra and Ramakrishnan, 1983a). The cationic losses, however, were invariably lower in the terrace agroecosystem, compared to jhum under a 5-year cycle, as seen in this study. If the total loss of nutrients, such as nitrogen and potassium, are calculated as a percentage of the total input of these through inorganic fertilizers, this works out to 56% for N and 28% for K. This loss is increased further (64% for N and 33% for K) in the second year of cultivation due to a decline in the physical characteristics of the soil. Thus this study (Mishra and Ramakrishnan, 1983a) shows that terracing is not a viable alternative from the point of view of fertilizer use efficiency.

16.6 Soil Fertility of Agricultural Systems and the Recovery Process

The depletion of soil fertility during the cropping phase of jhum and its recovery pattern during fallow regrowth has been considered for jhum cycles of 30, 10, and 5 years for the lower elevation (Ramakrishnan and Toky, 1981) and for cycles of 15, 10, and 5 years, along with terrace cultivation at the higher elevation (Mishra and Ramakrishnan, 1983b). The patterns for the jhum systems at both elevations are essentially the same and therefore the low elevation systems have been discussed here

in detail with only a brief reference to the high elevation systems where necessary.

16.6.1 Fertility During Cropping Phase

The physicochemical characteristics of the top soil are significantly altered by the slash and burn process. This process produces environmental changes, such as high insolation, subsequent changes in soil moisture and atmospheric humidity, and changes in soil and atmospheric temperature conditions from the clear felling. These changes and changes in soil chemistry are accentuated by low- or high-intensity burns.

The changes in soil carbon and nitrogen during the cropping phase was essentially the same and hence, only the data for carbon are shown here (Figure 16.1). There was rapid depletion during the early phases, followed by a recovery at the end of 365 days. The significant reduction in carbon and nitrogen soon after the burn under 30- and 10-year cycles is related to high-intensity burn. The soil under a 5-year cycle is less affected due to the low-intensity burn. These losses are from volatilization. During cropping, organic matter is lost through rapid decomposition from high insolation. The recovery at the end of 1 year is due to the decomposition of slash of the harvested crops and weeds. Juo and Lal (1977) showed that 16 t/ha/yr of dried plant material needs to be added to the soil during cropping under shifting agriculture in west Nigeria to maintain the soil fertility at a level comparable to that of a secondary forest. The decline in nitrogen losses during cropping is related to absorption by the crop species and losses through leaching, as discussed earlier. Our results suggest a rapid increase in the rate of nitrification after the burn. This increase may be due to a rise in pH and temperature (Ahlgren and Ahlgren, 1965) and removal of allelopathic inhibitors from the soil (Smith, et al., 1968). However, the losses continued in spite of this increase, and some recovery was observed only at the end of 1 year, though not to the level prior to the burn.

Phosphorus increase after the fire was only slight at lower-elevation jhum systems (Figure 16.1), and at higher elevations, there was a significant decline (Mishra and Ramakrishnan, 1983b). Others have reported no significant effect (Viro, 1974) or even an increase (Nye and Greenland, 1960; Stark, 1971). Though there are no obvious mechanisms for volatilization of phosphorous, Lloyd (1971) has reported massive losses from burning, which seem to agree with the present results. The rapid buildup of phosphorous a month after the burn may be due to release from the ash after the rains, increase in soil pH and consequent increase in microbial activity (Ahlgren and Ahlgren, 1971) and related mineralization of residual humus. This buildup was followed by a sharp decline due to crop uptake and other losses, followed by a recovery to a level higher than before the burn.

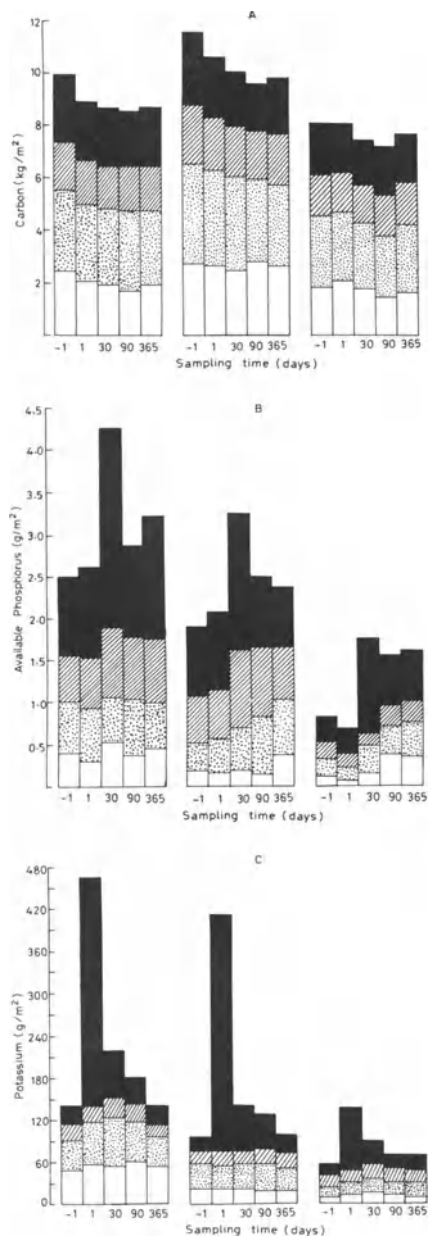


Figure 16.1. Changes in total quantity of carbon (A), available phosphorus (B) and potassium (C) within a soil column of 40 cm depth after burn and during cropping in sites under 30, 10 and 5-year jhum cycles. Dark portion of column, 0 to 7 cm; hatched portion, 7 to 14 cm; stippled portion, 14 to 28 cm; open portion 28 to 40 cm depth of soil. Sampling time indicates number of days before and after burn (after Ramakrishnan and Toky, 1981).

The importance of fire in slash and burn agriculture lies in the release of cations in one single flush at the surface of the soil. A high level of cations is maintained even after a year of cropping, despite losses from the system. Figure 16.1 shows only the pattern for potassium under lower-elevation jhum. Because this is generally true for both calcium and magnesium, the pattern for these two elements are not shown here (Ramakrishnan and Toky, 1981). The release of cations was highest under a long jhum cycle of 30 years and was minimal under a 5-year cycle, related to the quantity of slash. After an initial phase of release, depletion occurred, more markedly under a short cycle. Potassium release is markedly higher under a 10-year jhum cycle because *Dendrocalamus hamiltonii* is the predominant component of slash here. Under a 30-year cycle, calcium was markedly higher due to dicot trees being the chief source for the slash material at lower elevations.

In general, the nutrient quantities at different stages of cropping are lower under short jhum cycles at both elevations. At higher elevations, where the land is prepared into ridges and furrows, fertility changes are significant only on the ridges (Mishra and Ramakrishnan, 1983b). One of the chief conclusions is that the poorer nutrient status of the plots under short jhum cycles is partly responsible for the reduced crop yield discussed earlier.

The terrace agroecosystem studied at higher elevations (Mishra and Ramakrishnan, 1983b) is uneconomical from the fertility point of view for the following reasons: (1) the initial carbon level was significantly lower than even the preburn level under a 5-year jhum cycle, (2) nitrogen depletion continued up to the end of the two-year cropping period, and (3) cationic levels were low to start with and declined to even lower levels by the end of cropping. All of these nutrient losses occurred in spite of heavy fertilizer inputs into the system.

16.6.2 Fertility Recovery in Jhum Fallows

The recovery process for nutrients in the soil under both low- and high-elevation systems are essentially the same. For the elements C, N, P, K, Ca, and Mg, there was an initial phase of depletion, followed by 5 to 10 years of fallow development, and finally recovery of the system. At lower elevations (Ramakrishnan and Toky, 1981), where a 50-year fallow regrowth was also considered, the levels of C, N, P, and K are high due to release through litter, whereas Ca and Mg are lowest due to retention in wood and poor circulation through litter. Therefore, in Figure 16.2, the pattern for K and Ca are contrasted. The recharge of nutrients, such as Ca and Mg, in the soil pool seem to be exclusively fire dependent, whereas K release due to litter fall recharges the soil pool, resulting in a very high level in a 50-year fallow.

Dendrocalamus hamiltonii, which predominates in fallows of up to 20 years absorbs K rapidly, thus depleting the soil, but accumulating it in

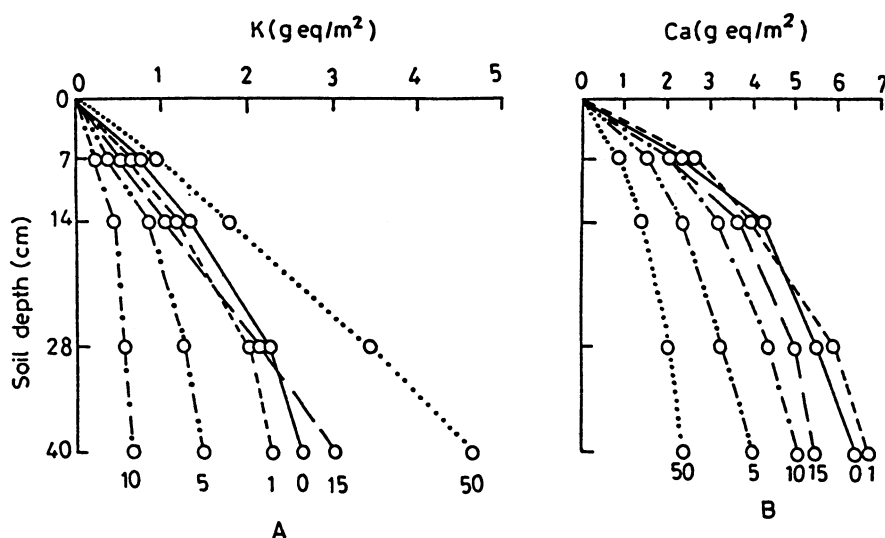


Figure 16.2. Changes in cumulative quantity of potassium (A) and calcium (B) within a soil column of 40 cm depth after fallows of various ages of 0, 1, 5, 10, 15, and 50 years (after Ramakrishnan and Toky, 1981). Reprinted with permission of Kluwer Academic Publishers.

biomass and releasing it subsequently through death and decomposition. These studies thus point to the necessity of maintaining a jhum cycle of 10 years or more in order to have a sufficient recovery of soil fertility for cropping.

16.7 Conclusions

Jhum, which is the chief agricultural system in the northeast hill region of India, is a way of life with the tribal population (Ramakrishnan, 1981; Ramakrishnan, et al., 1981a, b). In spite of the distortions brought about and ecological damage done as a result of a drastic reduction in the length of the jhum cycle, no viable alternative has yet been developed. Experimental terracing has failed to receive acceptance. Recently, a three-tier land management has been suggested as an alternative (Borthakur, et al., 1976), with forest cover on the top one-third of the hill slope, plantation/horticultural crops in the middle one-third of the slope and terraced cereal cropping along the lower one-third of the slope. These alternatives are likely to fail because they ignore the human element in terms of socio-economic and sociocultural factors.

Under the climatic, edaphic, topographic, and sociologic conditions prevailing here, jhum seems to be a viable land use, which has evolved over centuries, and from which the farmer can obtain all his basic needs

with practically no input except human labor. The other form of land use, namely the valley agroecosystem, is constrained because of topography, though it is ecologically efficient. Therefore, jhum should be adapted and altered rather than replaced by introduced agricultural technology from outside. In such an adaptation, the basic ingredients of jhum with a 10-year minimum cycle should be incorporated. The basic ingredients are (1) multiple cropping, which is ecologically and economically efficient from the point of resource use, and biomass production, which is recycled into the system as fertilizer; (2) weeds, which have an economically and ecologically positive role in the agroecosystem apart from their well-known role as competitors with crops; (3) agricultural systems with a high efficiency of nutrient cycling; (4) an internalized ability for pest and disease control; and above all, (5) a system based on the use of local resources rather than imported fertilizers, fungicides, and pesticides.

A 10-year cycle jhum should be a limited land use practice. In the present context, because a 10-year jhum cycle cannot be sustained due to land degradation, desertification, and increased population pressure (Ramakrishnan, 1981; Ramakrishnan, 1981a, b), the economy should be diverted to plantation/horticultural crops as a limited alternative land use along with forestry. The region is suitable for a wide variety of fruit crops. Rubber, tea, and coffee have been successful on an experimental scale. Such a three-pronged land use thrust with jhum, plantation/horticulture, and forestry on steep hill slopes should be able to meet the economic and social needs of the tribal population in the region.

In the wider context of agriculture in developing countries, such as India, it should be possible to replace the use of imported chemical fertilizers with local biofertilizers and to use available labor more efficiently for stability of the system. Because a large majority of the rural households are headed by small-scale and marginal farmers, such a shift in technology (small scale irrigation projects, biofertilizer, biogas technology and more efficient recycling of resources) seems to be more appropriate.

Integrated rural development should diversify primary production systems, developing the interlinkages in the different subsystems of the village ecosystem on a more scientific basis. Thus swine husbandry, for example, could be strengthened with better breeds for meat production. Fuel wood production could be augmented with fast-growing, native trees (Boojh and Ramakrishnan, 1982a, b; Ramakrishnan, et al., 1982) as well as better energy efficiency through appropriate technology. Social forestry with ecologically viable mixtures of native species (Ramakrishnan, et al., 1982) would meet other needs, such as timber. These strategies would help in conservation of the environment of these mountain ranges that are so important not only for the region, but also for the environmental quality in the northern plains.

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17. The Impact of Agrohydrological Management on Water, Nutrients, and Fertilizers in the Environment of the Netherlands

J.G. de Molenaar

17.1 Introduction

The Netherlands cover a land area of approximately 34,000 square kilometers of the northwestern European lowlands. With roughly 14.5 million inhabitants, all available land is intensively cultivated. Its history of agrohydrological management covers millennia; early attempts of drainage were undertaken as long ago as the Bronze Age, about 3,000 years ago. Today agrohydrological management, in interaction with the use of manure and fertilizers, substantially contributes to widespread land drainage and eutrophication. Another potential problem may be due to acid deposition through volatilization of ammonia. The impact is the more serious because of its diffuse character, compared with the influence of other activities. There is now hardly any part of the country that is not subject to the influence of water management in some way (Figure 17.1).

17.2 Outlines of Historical and Modern Agriculture

Agriculture has been practiced in the Netherlands for over 7,000 years since the early Neolithic. Well into the nineteenth century, farming was autarkic and rather diversified. Limited knowledge, technology, social

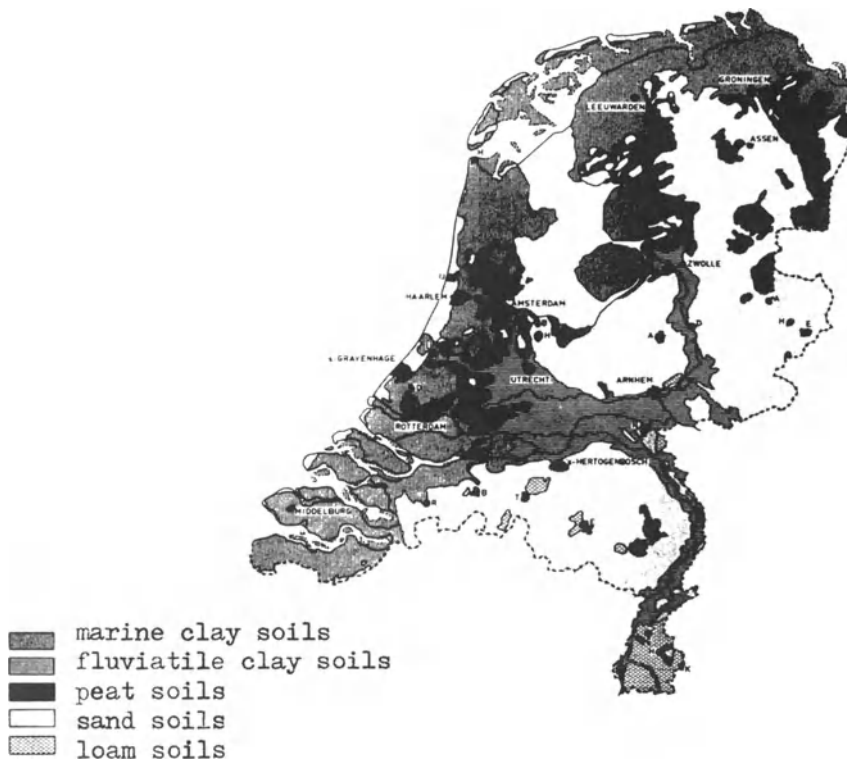


Figure 17.1. Major soil types of the Netherlands, according to Stiboka. Only the areas with sand soils and loam soils are well above sea level and not protected by dikes.

organization, and the like forced it to adapt to natural conditions, resulting in a high degree of diversity and stability in land use without drastically affecting the environment.

Farming historically combined arable crops and animal husbandry. Mixed farming developed into various regional land-use systems. These had as a basic pattern the farmstead, a small area of fertilized, arable land and pasture in relatively favorable condition with regard to soil, hydrology, and fertility, all surrounded by expansive areas for grazing, hay making, cutting sods, etc., on less favorable soils that were either dry or wet, or poor or heavy ground. The more extensively exploited fields provided the basis for the productivity of the intensively exploited arable and pasture lands by the supply of nutrients. They were thus subject to constant nutrient loss, such that by 1900, two-thirds of the country showed a decrease in fertility (Figures 17.2 and 17.3).

In our century, the Netherlands became a predominantly industrialized country. Technological, socioeconomic and demographic developments,

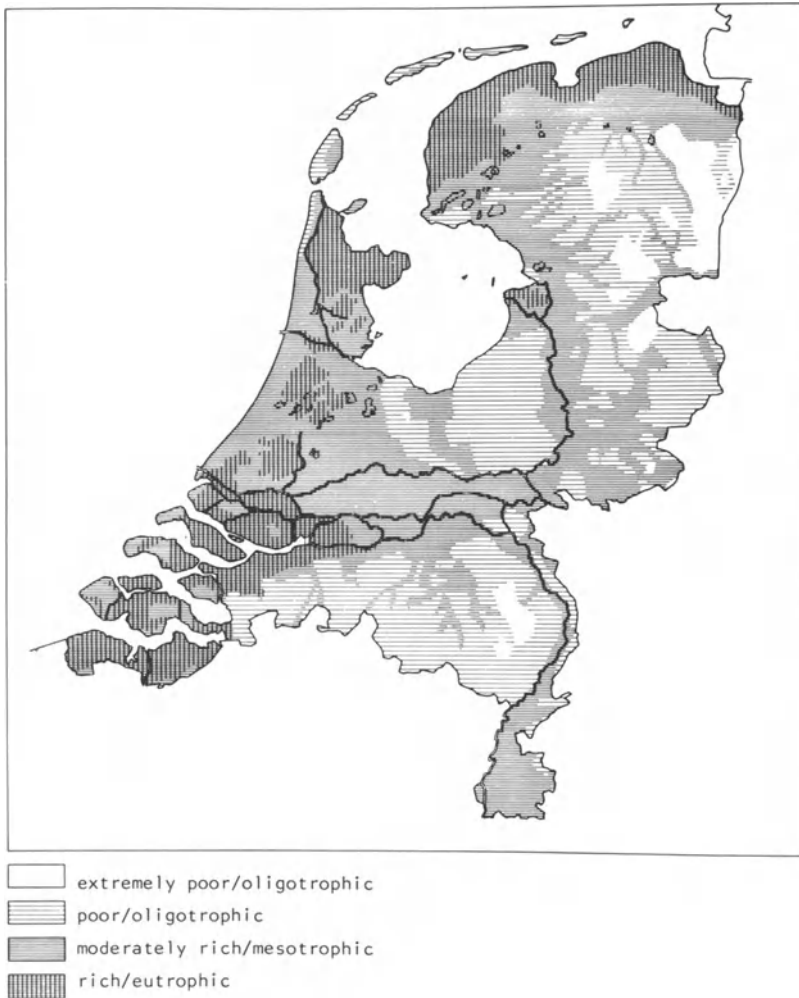


Figure 17.2. Original, natural soil fertility in the Netherlands (Smittenberg, in Van der Marel and Dauvellier, 1978).

together with developments elsewhere in the world influencing the Dutch situation, had rapidly increasing impacts on the environment.

Modern agriculture changed into an open system with a high input of nutrients, animal fodder, and energy from other parts of the world. A shortage of manure, once a critical problem, became a surplus, creating a problem regarding both public health and the environment. Former restrictions of topography, hydrology, and soil could increasingly be dealt with using modern technology. Formerly extensively exploited areas (heath, wet hayland) lost their agricultural function, became known as

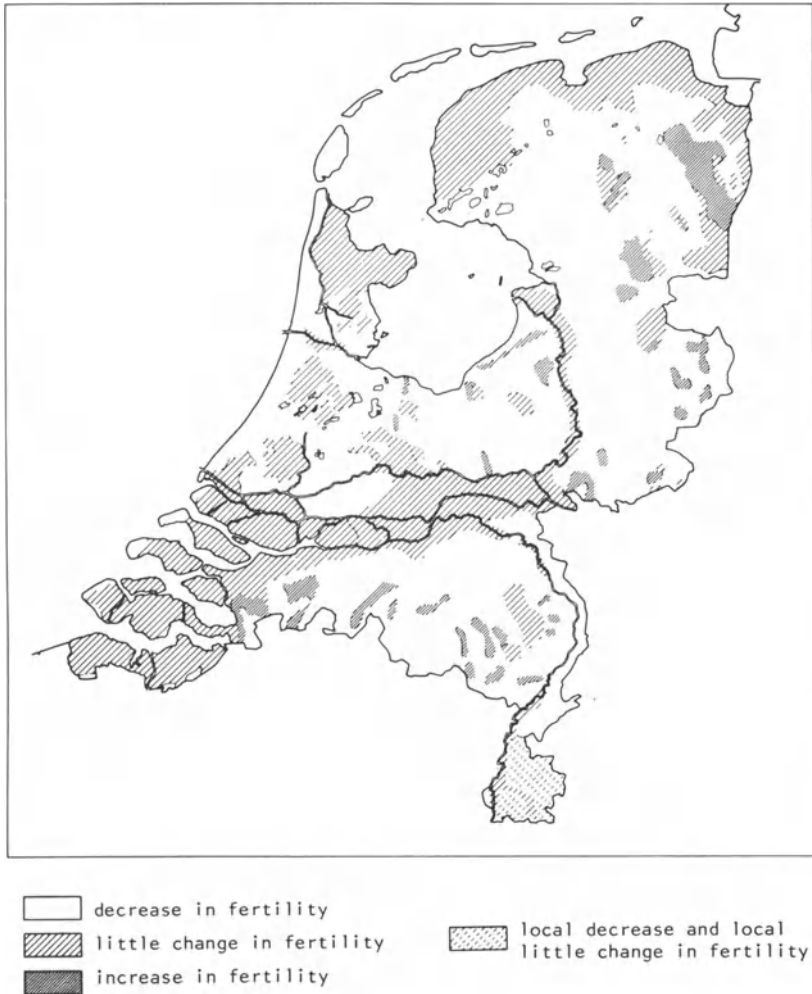


Figure 17.3. Impact of human influences on soil fertility in the Netherlands about 1900 (Smittenberg, in Van der Maarel and Dauvellier, 1978).

“waste land,” and were recultivated or reclaimed. The heathland area decreased in the present century by about 90%; wet, oligotrophic haylands by an even higher percentage. The general outcome has been an overall intensification and an enlargement of scale, including short-term adaptation to internationalized market and trade policy conditions. Increasing spatial uniformity and increasing temporal instability replaced old-fashioned spatial diversity and temporal stability in land use (Bakker, 1958; Meihuizen, 1964; Leeuwen, 1966; Bouwer, 1970; Wethoff et al., 1970;

Lambert, 1971; Slicher van Bath, 1978; Smittenberg in Van der Maarel & Dauvellier, 1978; Keuning, 1979).

17.2.1 Water Management: Western Part of the Country

The western part of the country covers about three-quarters of the land area of the Netherlands and consists of holocene clay and peat deposits. Its present elevation ranges from slightly above to about 5 m below mean sea level (Figure 17.1). In the absence of dunes, dikes, and modern water management, it would be flooded at high sea and river levels.

Two to three thousand years ago, it was a poorly drained region of peatland, tidal marsh, and river lands a little above sea level. To the west, it was protected against the sea by a coastal rampart of dunes and to the east and south it passed into the higher sandy grounds of the country.

The elevated sites along the coast (dune ridges, salt-marsh bars) and along the rivers and streams (levees, early Holocene river dunes) were occupied at an early date. The perils of marine transgression were met by raising artificial mounds (Boersma, 1972), especially in the northern coastal salt marsh area, between 500 BC and A.D. 800 to 1,000. This could not prevent considerable loss of land, until the increase in population, development of social organization, and relative prosperity permitted the building of dikes. This defense was fairly well under way by A.D. 1,000 (Giffen, 1964), when the invention of simple, tide-operated sluices greatly facilitated the drainage of clayey soils along the estuaries and tidal streams. The period A.D. 1,000 to 1,300 witnessed the organization of self-governing polder and drainage boards ("waterschappen"), which took the responsibility for dike maintenance and water control (Fockema Andreae, 1952; Linden, 1977).

The cultivation of the central peatlands behind the dunes occurred soon thereafter, starting with the occupation of the inner dunes and the intersecting rivers and streams. The necessary drainage and the initial tillage caused rapid compaction and oxidation of the peat, resulting in subsidence of the soil surface. Eventually, when free drainage became hampered and the fertilizing effect of peat mineralization ceased, the land use changed to poor pasture and hayland. The reclamation was subsequently extended. The newly reclaimed area suffered in due time the same fate, and so on until there was no more area to reclaim; the limits of reclamation seemed to have been met (Hofstee and Vlam, 1952; Linden, 1955, 1982; Gottschalk, 1956a, b; Lamber, 1971; Edelman, 1974). The larger part of the peatland thus became a waterlogged, wet grassland area characterized by dairy farming and large-scale oligotrophication or maintenance of oligotrophy due to the continuous nutrient removal from the expansive haylands. The management of drainage ditches included the use of plants and mud from these ditches (alone or mixed with manure) to dress the land. This caused an increasing widening of the ditches;

in various areas this resulted in almost equal areas of land surface and water surface.

On soils with only a thin peat cover, drainage and cultivation caused the entire disappearance of this top layer. It is only preserved in some places below early, lasting structures like burial mounds and old buildings, such as churches (west Friesland, Groningen, western Noord-Brabant, etc.; Edelman, 1958, 1974; Pons and Van Oosten, 1974).

Somewhat similar conditions existed naturally in the clay region of the branches of the Lower Rhine and the Meuse (Modderman, 1955). Sandy to light clayey levees along the winter beds and former courses embraced lower "komklei" areas or "velden," which are vast stretches of poorly drained heavy clays of back swamp lands. Embankment of rivers increased the relative rise of their summer and winter beds by fixing the stream courses and concentrating sedimentation. This aggravated the hampered drainage of these komklei areas, with the same effect as the soil surface subsidence in the western peatlands. Comparable conditions existed in the early-occupied, coastal, salt-marsh areas adjacent to the high Pleistocene hinterland. The free drainage of these low areas became gradually hampered by the rise of the outer salt marsh bars through the process of relative sea level rising. Successive diking of new marshes, having reached sufficient height above the gradually rising sea level, reinforced these conditions; each new embankment had a slightly higher level, the older polders thus became more difficult to drain.

The wind-driven water mill, introduced in the late Middle Ages, provided a tool to keep the half-drowning reclamations from further deterioration and abandonment, though not much more than that. From the sixteenth century onwards, a complex of developments in technology, economy (especially commerce), agriculture, and population swelled the demand for peat as a fuel. This resulted in further land loss, aggravated by increasing erosion, threatening even Amsterdam. On the other hand, these developments also swelled the demand for land. This led to reclamation of a series of lakes (Trouw, 1948; De Bakker, 1950; Van Schail, 1969; Edelman, 1974; De Zeeuw, 1978; Colenbrander, 1986; Figure 17.4). The last polder so far, Zuidelijk Flevoland (43,000 ha) in the former Zuyder Zee, was drained in 1968.

The actual amount of drainage was shallow, and was soon followed by the relative subsidence of the soil surface. Drainage focused on lowering the water level in summer. In the central, western peat-grassland area, the aim was generally to keep the ditch water level just a few dm below the land surface. In winter, it could reach or exceed that surface. Until less than a century ago, large areas (e.g., in Friesland, the komklei parts in the area of the great rivers) were frequently entirely flooded in winter time. On the other hand, water was frequently supplied from rivers and streams during dry periods in summer.

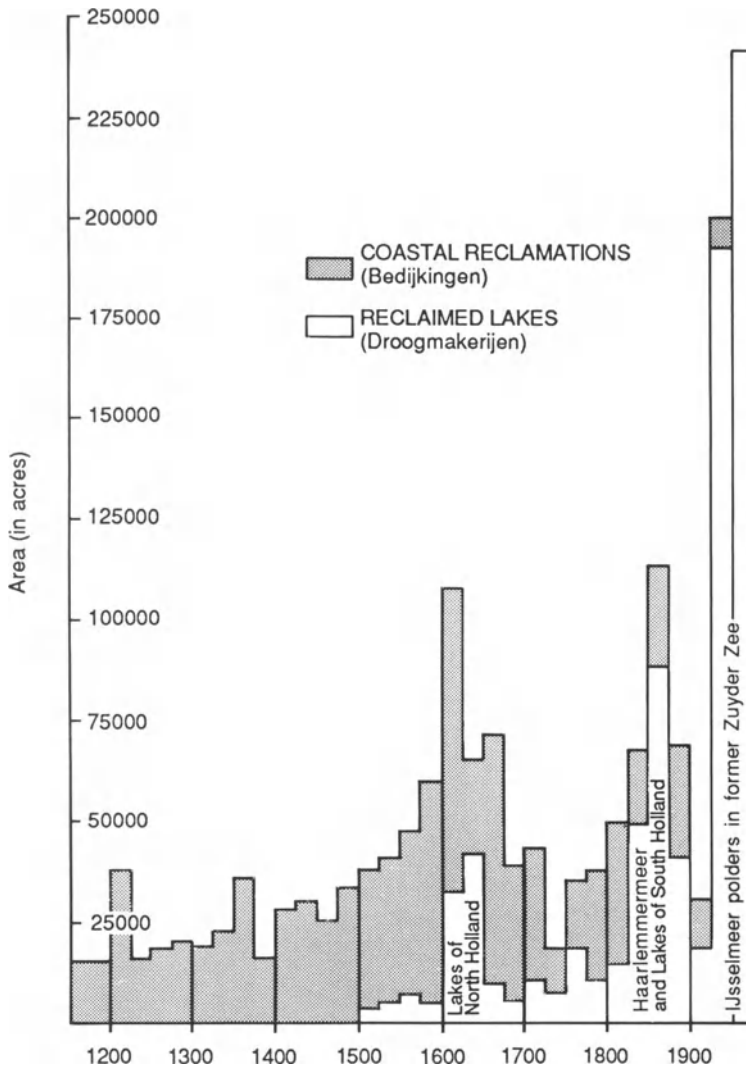


Figure 17.4. Land reclamation in the Netherlands (data updated from Trouw, 1948 and Wagret, 1968).

This regime lasted until steam engines came into use for drainage in the second half of the nineteenth century. Their capacity enabled a more stringent water management. The winter drainage was improved, and sometimes also the summer drainage. Figure 17.5 illustrates the winter drainage conditions in the middle of this century, when electric and diesel-pumping engines became predominant. From then on, the ditch water level was drastically lowered, in particular the winter level (Table 17.1),



Figure 17.5. Average winter groundwater levels in the Netherlands in the middle of this century. a. 0 to 20 cm below surface. b. 20 to 40 cm below surface. c. > 40 cm below surface. (International Institute for Land Reclamation and Improvement, 1960).

to the extent that the natural winter/summer fluctuation pattern was often even reversed.

Drastically lower winter levels are reached by intensification of winter precipitation surplus discharge. This is often accompanied by a water shortage during the summer when precipitation is deficient. This requires the use of alternative surface-water supplies for agriculture and other

Table 17.1. Average subsidence in relation to drainage in the peat grassland area in the western Netherlands

Approximate period	Desired ditch water level (dm below land surface)		Average land subsidence (mm/year)
	Summer	Winter	
Before 1875	2-3	≤0	2
1875 to 1950		2-4	4
After 1950		7-10	10-14

Source: De Molenaar, 1980.

aspects of water management, such as abatement of salt intrusion (through shipping routes) and some internal salinization (upwelling of brackish deep groundwater due to deeper drainage). The supply of water in summer is derived mainly from the Rhine and its tributaries. This hypertrophied, polluted water has been increasingly spread over the area, reaching places where once only oligotrophic rainwater was found. In addition, sprinkle irrigation is practiced more and more, using surface water as well as groundwater.

17.2.2 Water Management: Eastern Part of the Country

The eastern part of the country consists of mainly pleistocene sandy soils well above sea level. These high grounds in the east and south probably have an even longer history of occupation. The establishment of permanent crop lands occurred by and large by the late Middle Ages (see survey in Lambert, 1971).

The area as a whole drains freely. Soil and water conditions for a long time did not call for drastic measures other than the use of contemporary knowledge. The natural, surface discharge systems were only slightly modified in the past to deal with the increased peak discharges resulting from hydrological changes caused by deforestation and exploitation of moors and bogs. Sometimes new water courses were dug to link isolated depressions with existing drainage channels, to suit water mills, etc.

Heathland and arable land on relatively dry sites drained subterraneously. Moist pasture and wet hayland along natural water courses were drained by ditches and trenches, except for part of the swampy grassland along the lower courses of larger brooks. There, periodic flooding with relatively enriched water was preferred and even promoted, often being lengthened by setting weirs and throwing up low dikes, even into this century. The vast stretches of raised bogs, mires, swampy forest, and moist heath in the east and south remained relatively untouched for a long time. Their cultivation started gradually in the Middle Ages and lasted until the present century. In the Netherlands, only 3.7% of the original raised bogs remain today.

The basic pattern of land use (Naarding, 1947; Roo, 1952; Edelman and Edelman-Vlam, 1960; Bouwer, 1970, 1985) was regionally adapted to the scale of physiographical variation and social conditions, either in individual farmstead holdings (*hoeven*) or in strictly organized farmers' communities (*marken*, *maalschappen*). Essential in the system was the relatively large area of heathland, being the main source of manure (sheep dung, sods) for the arable. There was rigid control of the use of the common areas, especially of the common heath, with strictness reflecting a village's lack of resources. These *marken* organizations did not break up until the 19th century, when the introduction of chemical fertilizers and the importation of cheap Australian wool drastically diminished the agricultural value of the heath. The breaking up of the *marken* was enforced by the *Markenwet* of 1886 and was completed about World War I. The recultivation (in part also reforestation) of the formerly extensively exploited heathlands continued until about 30 years ago and led to the agrohydrological opening of this region. This included a drastic lowering of the groundwater table in areas once poorly drained because of topographical and geohydrological reasons. Initially, the increasing water storage capacity of the topsoil buffered the peaks in the removal of precipitation surplus. Recent, deeper drainage should increase this buffering,



Figure 17.6. Drainage conditions in the Pleistocene province of Drenthe in 1974 (Werkgroep Regionaal Geohydrologisch Onderzoek in de provincie Drenthe, 1978).

but is counteracted by more extensive agrohydrological demands impacting the depth and constancy of the water table after more intensive drainage. The consequences of these modern demands are reflected in the extent of drainage improvement (Figure 17.6).

Recent deeper drainage and intensified discharge have created or aggravated the need for agricultural water supply during precipitation deficient periods in summer. This need is relieved by inputs supplied by



Figure 17.7. Areas with agricultural surface water supply in 1976 (hatched area; Ministerie van Verkeer en Waterstaat, 1985; from data of Unie van Waterschappen).

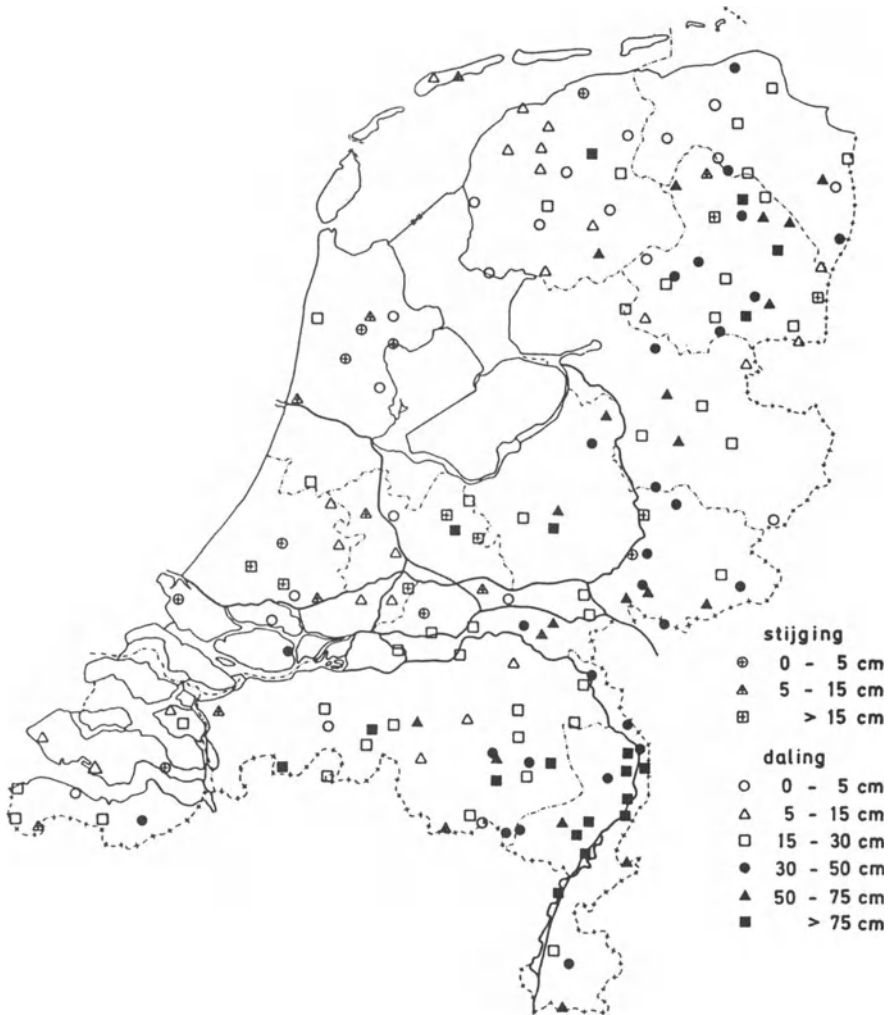


Figure 17.8. Changes in average groundwater levels between 1956 and 1960, and 1973 and 1977; stijging = rising, daling = lowering (Ministerie van Verkeer en Waterstaat, 1985; from data compiled by Dienst Grondwaterverkenningen TNO).

upstream water transport. The imported water, mostly hypertrophied and contaminated surface water (mainly from the Rhine River), not only adds to the environmental impact of these technical inputs on the major surface waters, but also becomes widely distributed over formerly oligotrophic areas (Figure 17.7; compare with Figures 17.2 and 17.3). In addition, surface water and groundwater is used for sprinkle irrigation infiltration. This brings other agriculturally undesirable side effects, such

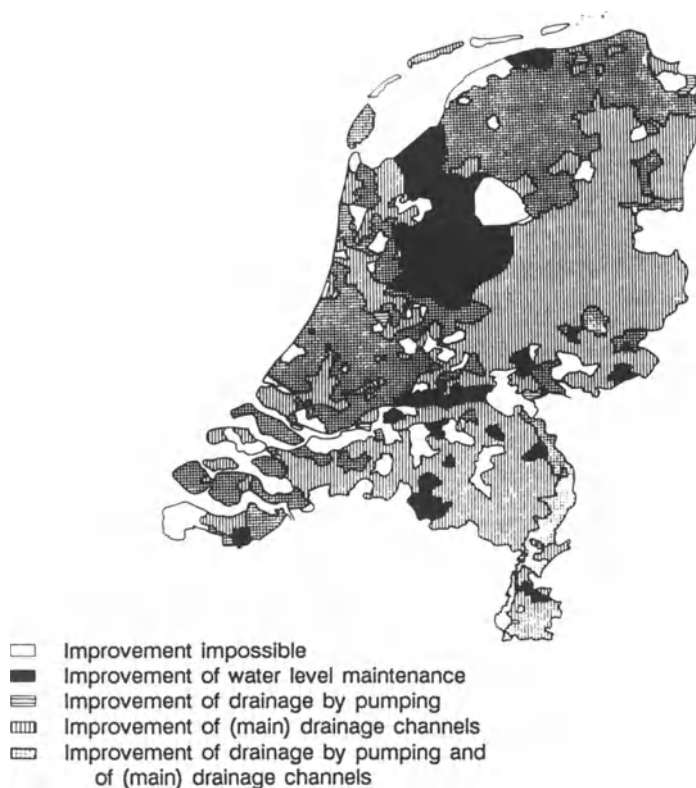


Figure 17.9. Inventory of the agrohydrological conditions in 1975/1976; rectangles represent types of improvements possible at acceptable costs for each municipality in the Netherlands (Ton and Lourens, 1978).

as excessive lowering of the water table, placing all the more emphasis on allochthonous surface water supplies.

17.3 Extent of Water Management

At present there is virtually no part of the country that is not subject to recent lowering of the groundwater level (see Figure 17.8). (Note: occasional rise of the groundwater is mainly concentrated in peatland areas, due to subsidence following deeper drainage.) Possibilities for agrohydrological improvement are presented in Figure 17.9, whereas Figure 17.10 gives a prognosis for the change in groundwater levels in the near future (for prognoses which take into consideration various scenarios for additional local water supply, see Ministerie van Verkeer en Waterstaat, 1985).

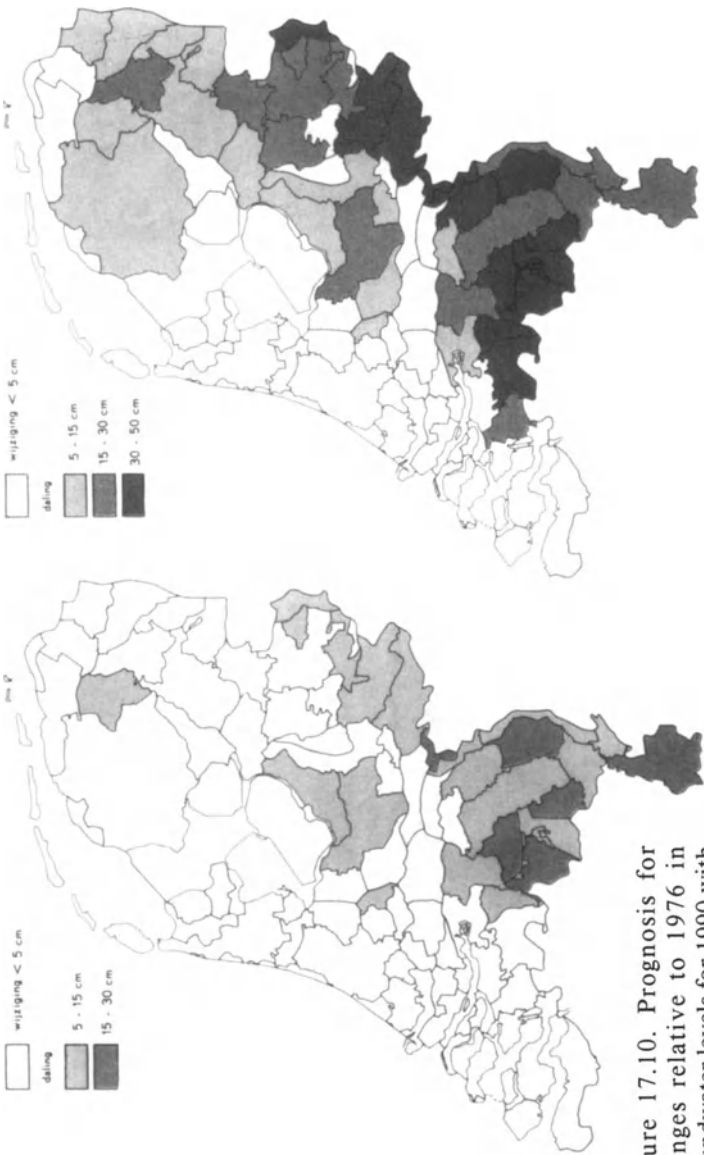


Figure 17.10. Prognosis for changes relative to 1976 in groundwater levels for 1990 with no policy changes for an average year (top) and for an extremely dry year (bottom); wijziging < 5 cm = change < 5 cm; daling = lowering (Ministerie van Verkeer en Waterstaat, 1985).

Table 17.2. Projection of the percentage of agricultural area sprinkle irrigated in the Netherlands with unchanged policy

	1976	1990
Area sprinkled with surface water (%)	10	23
Area sprinkled with ground water (%)	4	25
TOTAL (%)	14	48

Source: Ministerie van Verkeer en Waterstaat, 1985.

Table 17.3. Annual agricultural water demand (in 10^6 m^3) during the period 1976 to 1990, with no policy change and with/without water supply plans

	Dry year ($\times 10^6 \text{ m}^3$)		Extremely dry year ($\times 10^6 \text{ m}^3$)	
	With water	Without water	With water	Without water
Surface water demand	1268	1603	1960	2690
Ground water demand	145	890	250	1545

Source: Ministerie van Verkeer en Waterstaat, 1985.

Sprinkle irrigation gained dramatic momentum in the very dry summer of 1976. In that year, over $650 \times 10^6 \text{ m}^3$ water (69% from surface water, 31% from groundwater) was used for sprinkling an area of over 220,000 ha with an average amount of 297 mm/ha (De Wilde and Linthorst, 1978). Tables 17.2 and 17.3 give sprinkling prognoses for the near future. The total national demand for groundwater in 1976 was $1207 \times 10^6 \text{ m}^3$, and for 1990 it is estimated at 1787 to $1929 \times 10^6 \text{ m}^3$ (Ministerie van Verkeer en Waterstaat, 1985). The extent and influence of surface water supply and some short-term prognoses are given in Figure 17.11.

17.4 Water Management, Nutrient Supply, and Fertilizing

Water management is closely linked with fertilizing and other agricultural activities. It is a component of the entire complex of intensification. Water management is also a prerequisite for agriculture in the greater part of the country. Modern, drastically deeper drainage is considered necessary for intensification, including heavy mechanization, increased cattle densities, and profitable use and efficient application of liquid manure and fertilizers. Drainage also provides the advantage of an earlier drying and warming of the soil, as well as an extra supply of nutrients through the increased mineralization of organic soil material (de Molenaar, 1980; Schothorst, 1982). In grasslands, on peat soils, for instance, lowering of the groundwater table (ditch water level 8 to 10 dm below soil surface)

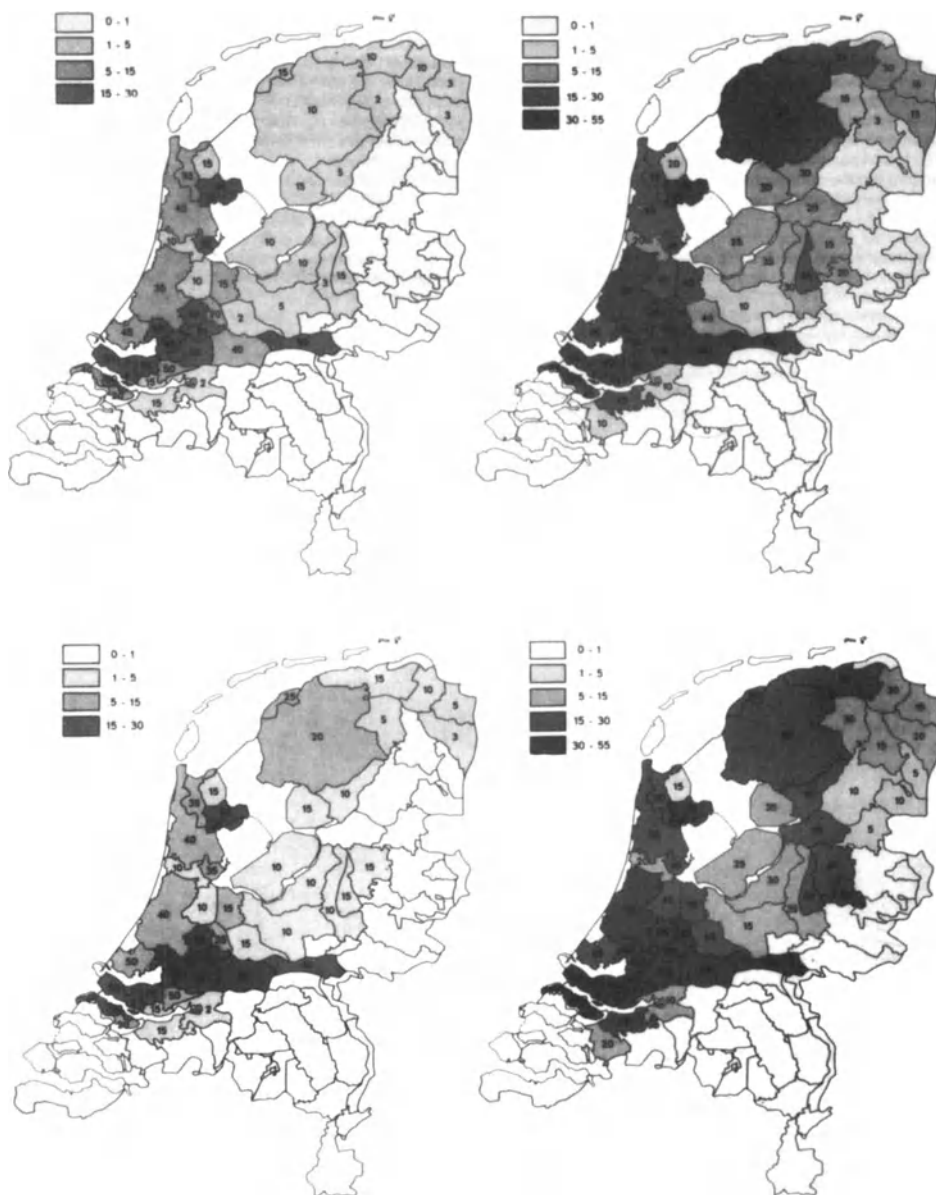


Figure 17.11. Average percentages of Rhine water in the Tertiary surface-water system in an average (left) and an extremely dry (right) year; for 1976 (above) and 1990 (below), under unchanged policy. Numbers in the districts on the maps indicate maximum percentages (Ministerie van Verkeer en Waterstaat, 1985).

may result in an additional supply of nitrogen ranging from 100 to 600 kg/ha/year, out of which only one-about half is used by the plants (Schothorst, 1977). A considerable amount of other mineral constituents, such as sulphate, are also used (Steenvoorden and Oosterom, 1975). In mineral soils, deeper drainage results in an increased availability of nutrients by decomposition of organic matter; increased nitrifying activity; and chemical, physical, and biological weathering of the deeper soil layers. In clay soils, it has been estimated that up to an additional 30 kg N becomes available by eliminating any days in spring during which the groundwater level is less than 30 cm below the surface (Sieben, 1964). For the influence of deeper drainage on other aspects, e.g., irreversible desiccation of the top soil and the agricultural quality of grassland, see de Molenaar (1980) and Baaijens and de Molenaar (1982).

Water deficits during the summer are overcome by supplying additional water. However, applying water to the surface only mitigates the desiccating impact of deeper drainage to some extent, and it reinforces possible eutrophication impacts as well. The use of ground water for irrigation aggravates deep drainage as well.

17.5 Nutrient Supply and Fertilizers

The general farming systems that lasted until about 1900 showed a general trend of nutrient loss over large areas due to the constant shortage of fertilizer (Figure 17.3). This limitation eased with the introduction of inorganic fertilizers. The increasing production of manure in the second half of this century brought the new problem of manure surplus, usually applied as liquid manure. Inorganic fertilizer is applied as well. The former trend of oligotrophication thus has turned into a trend of overall eutrophication (Figure 17.12).

Table 17.4 gives the total available manure and fertilizer in 1984. The production of manure varies regionally (Figure 17.13) and is concentrated in oligotrophic, recharge, or hydrological source areas (Figures 17.1–17.3). In such areas of concentrated intensive husbandry (“bio-industry”), application of considerable overdoses is common. Fertilizer is still applied in many cases to balance the nutrient supply, to offset the fact that much of the winter production of manure is not efficiently applied because of limited storage capacity.

The national nitrogen balance for the year 1985 shows a difference between N-input (fertilizer and imported fodder) and N-recovery (output in products) of 662×10^6 kg. The phosphorus balance reveals a surplus of 76×10^6 kg and the N-surplus corresponds to an average of over 300 kg N/ha of agricultural land (Meeuwissen and Van der Meer, 1988). For intensive dairy farming from 1983 to 1986, the surplus was 477 kg N/ha/year (Biewinga et al., 1987).

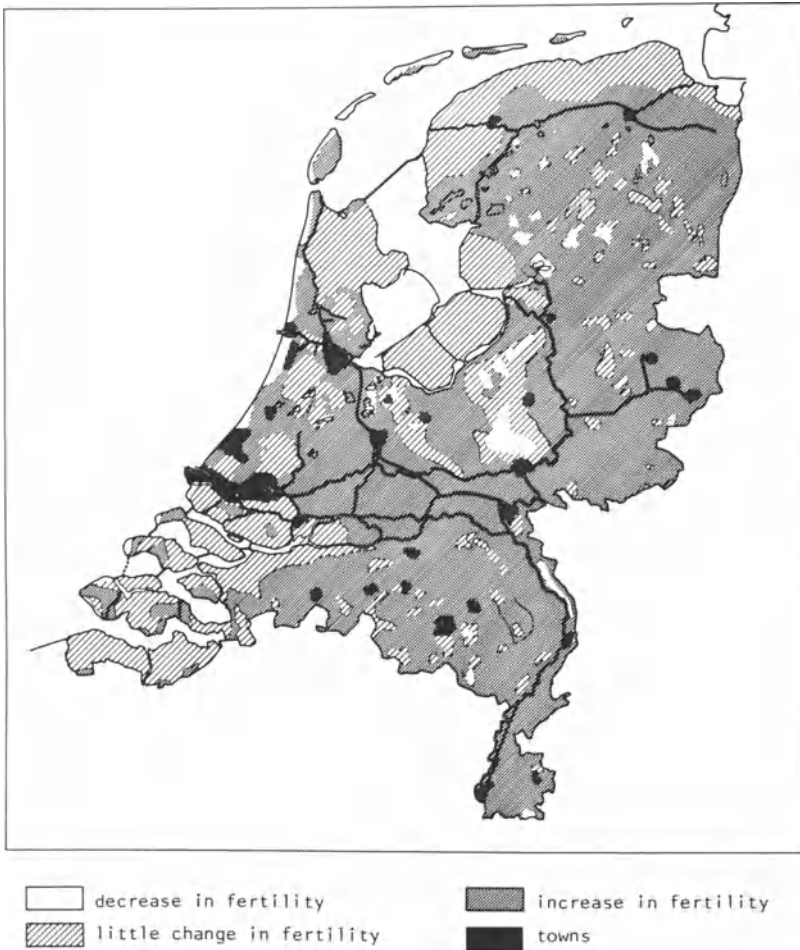


Figure 17.12. Impact of human influences on soil fertility in the Netherlands around 1975, compared to natural conditions (Smittenberg, in Van der Maarel and Dawvellier 1978).

The surplus nutrients may be emitted into the environment by air and water. Water management plays a role, apart from the evident interaction between drainage level and land use intensity, through the transport of fertilizer constituents, surface-water distribution (discharge and supply), and the availability of nutrients for the plant in the interaction between groundwater level and soil. The effect on groundwater quality has been known since the middle of the past century (Gunning, 1853). For the sake of brevity, the following will only touch on the macronutrients ni-

Table 17.4. Total availability and average availability for the agricultural area of nitrogen and phosphate in 1984

	N_{tot}^a (tons)	N_{eff}^b (tons)	P_2O_5 (tons)	N_{tot} (kg/ha)	N_{eff} (kg/ha)	P_2O_5 (kg/ha)
Manure	481	289	239	238	143	119
Fertilizer	478	478	87	238	238	43
Total		767	326		381	162

Source: Centraal Bureau voor de Statistiek, 1986.

$^a N_{\text{tot}}$ = total N.

$^b N_{\text{eff}}$ = effectively available N in manure, compared with the effect of N in fertilizer (i.e., 60%).

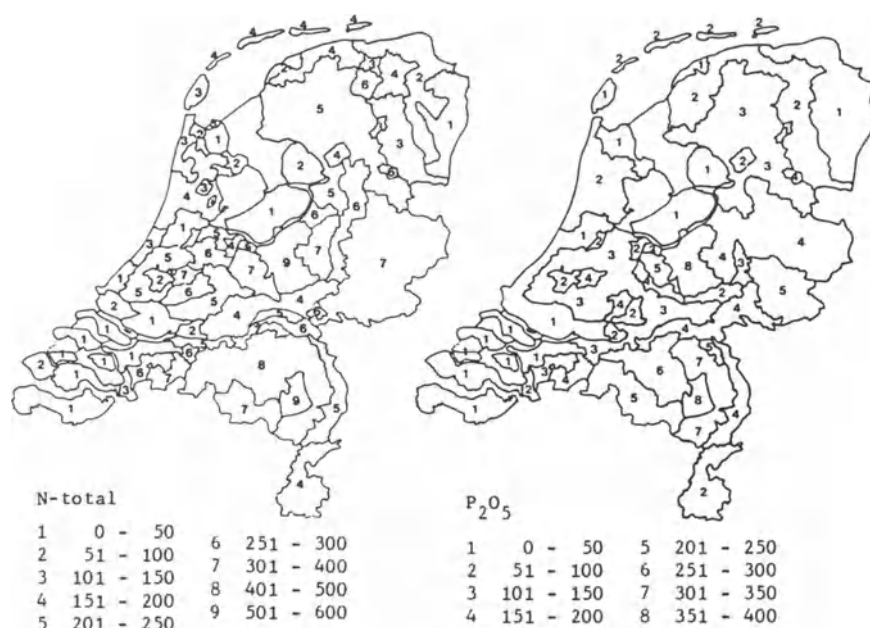


Figure 17.13. Manure production (kg/ha) in 1980. Recalculated from data of Centraal Bureau voor de Statistiek (1982). Production of cattle in the stable period of 180 days is doubled to get the annual production.

trogen and phosphate. It should be kept in mind that many other factors also contribute (e.g., household sewage).

17.5.1 Leaching

Leaching depends on the amount of precipitation, soil texture, and soil moisture content. It is concentrated in the period of net precipitation

surplus, i.e., from mid-August through March. However, considerable leaching may also occur in the net precipitation deficit period through drought cracks in clay and peat soils.

Nitrogen leaching concerns almost exclusively nitrate. The process depends on factors such as soil type and agricultural land use (de Molenaar, 1980; Kolenbrander, 1981). Research in the Netherlands so far has concentrated primarily on sandy soils, where applying manure in winter and spring on cropped land, in doses equivalent to or surpassing the crop demand, leads to the leaching of 20 to 25% (occasionally up to 40%) of the total N-supply (Steffens and Vetter, 1983; Oosterom, 1984; Oosterom and Steenvoorden, 1984; Van der Veen, 1984).

Nitrogen leaching is restricted by shallow groundwater levels, owing to a higher capillary rise, increased supplementary superficial discharge (interflow and runoff), and increased denitrification (anaerobic conditions (Steenvoorden, 1983; Duynisveld and Strebel, 1984). Under average drainage conditions, it is assumed that up to one-half of the leached N is lost in the subsoil by denitrification. In less aerobic to anaerobic groundwater, N usually occurs as ammonium.

National groundwater quality monitoring revealed twenty-eight drinking water pumping stations (out of about eighty) showing groundwater with nitrate concentration surpassing the European Economic Community (EEC) health norm of 50 mg/l (i.e., 11.3 mg N/l). Under cropped land, the upper groundwater reached an average concentration of 84 mg/l, with local values up to 1000 mg/l (CRM, 1986). Values under grasslands are usually lower. Figure 17.14 gives an indication of the distribution of N-concentrations in groundwater in the Netherlands (see also de Molenaar, 1980; Advies beperking uitrijperiode dierlijke meststoffen, 1986).

Phosphate in liquid manure amounts to 2 to 9.4% (or 2 to 6.6% dry weight) and is approximately 80% inorganic and 20% organic (Sluijsmans et al., 1978). Phosphates are readily adsorbed to the soil complex until the adsorption capacity is saturated. Adsorption depends on a series of conditions, such as soil texture (see de Molenaar 1980 for a survey). Presently, there are areas where the soil is P-saturated to a depth of 100 cm, with P-concentrations in the upper ground water ranging from 38 to 81 mg P/l (Lexmond et al., 1982). Organic P-compounds may leach relatively easily, especially P-humus complexes. The total area of relatively heavily manured crop land with P-saturated topsoil is at present close to 30,000 ha (Breeuwsma and Schoumans, 1986).

Drainage conditions are important because P-adsorption in water-saturated soil is restricted. Thus, P-leaching will increase when the P-adsorption front approaches the average water table. The risk generally increases, in contrast with the risk of N-leaching, with a shallower groundwater level. In such conditions, the risk of P loss to surface waters through interflow and surface runoff also increases.

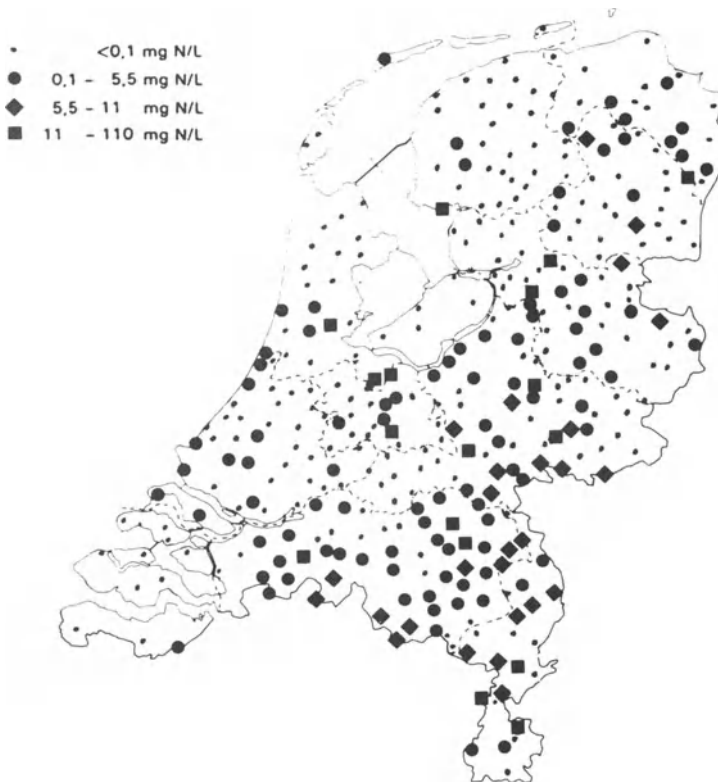


Figure 17.14. Nitrate in ground water at 9 m below the surface between 1979 and 1984 (Centraal Bureau voor de Statistiek, 1986).

17.5.2 Superficial Discharge

Shorter precipitation discharge routes, complementary to the deep discharge involved in leaching, are surface runoff, interflow (shallow groundwater flow), and interception of percolating water by drain pipe systems. This superficial discharge depends on soil type (Table 17.5 and Figure 17.1), drainage resistance, drainage conditions, and precipitation regime (Steenvoorden and Buitendijk, 1980; Buitendijk, 1986; Nijboer, 1986; Wind, 1986), and is concentrated in December, November, October, and January from most to least respectively. It also involves, next to the loss of macronutrients and other chemical compounds, the emission of organic particles that affect the amount of available oxygen in surface waters. In regard to the influence of drainage conditions and overall N-emission, superficial discharge of nitrogen and leaching of nitrogen react differently, and there are indications that with shallower drainage the superficial discharge increases less than the leaching decreases.

Table 17.5. Average surface discharge from sand, clay, and peat soils at different drainage levels

Drainage level (cm)	Water discharge (mm)	
	Sand and clay	Peat
– 30	60	150
– 60	15	70

Source: Advies beperking uitrijperiode dierlijke meststoffen, 1986.

The total phosphate concentration in uncontaminated groundwater in sandy areas is maximally 0.2 mg P/l, but with P-saturated soil where pig slurry is applied, the load is approximately 90 mg P/l (Lexmond et al., 1982). The consequences of a uniformly restricted, superficial, shallow discharge through the P-saturated zone are considerable, but if the topsoil is undersaturated, they are limited. In this context, it is noteworthy that approximately 20,000 ha of relatively heavily manured maize-cropped land (15% of the present area) are estimated to be P-saturated to the depth of the mean highest groundwater level (Breeuwsma and Schoumans, 1986). The maximum P-load of grassland is estimated at approximately 5 tons P_2O_5 /ha. The P-adsorption capacity above the mean groundwater level in shallow-drained to moderately deep-drained sandy soils is estimated at 2 to 7 tons P_2O_5 /ha, which refers to 200,000 ha, or 50 to 60% of the Dutch grassland area. P-saturation to this level is probably restricted to such sandy soils, because P application in clay and peat areas should be lower (Advies beperking uitrijperiode dierlijke meststoffen, 1986) (see also Table 17.6).

17.5.3 Volatilization

Ammonia volatilization contributes to eutrophication and, in interaction with other air contaminants, to acid deposition. The total nitrogen content of liquid manure ranges from 4.4 to 9% (i.e., 4.6 to 15% dry weight; Sluijsmans et al., 1978). Approximately 40 to 60% of this nitrogen is ammonia. Volatilization of the ammonia content may vary from 24 to 33% in 6 to 7 days (liquid dairy manure; Beauchamp et al., 1982) to 61 to 99% in 5 to 25 days after application (dairy manure; Lauer et al., 1976). Some ammonia volatilization may also result from the application of inorganic fertilizer.

The emission in the Netherlands for 1982 from agricultural sources is estimated at 137,500 tons (93% from manure, 7% from fertilizer) of a total emission of 154,000 tons (Buijsman et al., 1984). The average total atmospheric deposition of nitrogen is approximately 44 kg N/ha/yr; between one-half and about two-thirds of the wet deposition is attributed to ammonia/ammonium (Aalst and Diederer, 1983; KNMI/RIV, 1983).

Table 17.6. Estimated annual P-deposition as phosphate into surfacewater through groundwater flow

	Deep drainage			Shallow drainage		
	Groundwater flow (mm)	(mg/l)	P (kg/ha)	Groundwater flow (mm)	(mg/l)	P (kg/ha)
Superficial discharge	0	—	0.0	10	90	9.00
Deep discharge	300	0.2	0.6	290	0.2	0.58
Total	300		0.6	300		9.58

Source: Advies beperking uitrijperiode dierlijke meststoffen, 1986.

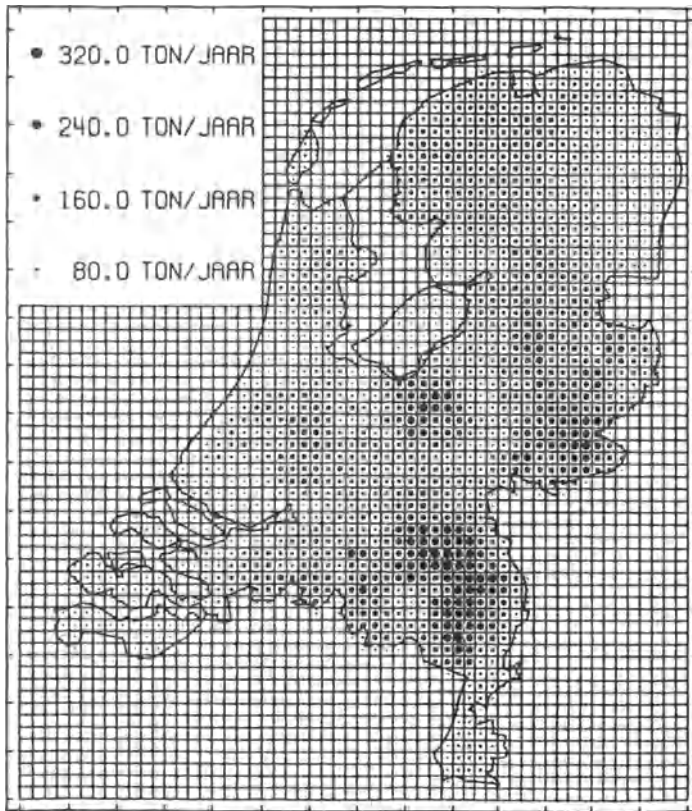


Figure 17.15. Total animal ammonia emission (tons/year) in the Netherlands; grid cells $5 \times 5 \text{ km}^2$. Buijsman et al., 1985.

There is considerable regional variation in emission, the balance between the constituents in N-deposition, and their origin (Figure 17.15). The first results of national groundwater quality monitoring showed a doubling of the number of sites with a pH below 5 (CRM, 1986).

The water regime and management have little influence on volatilization as such (neglecting the influence of drainage level on the ability to apply liquid manure), unless manure is plowed in or injected to limit emission into the atmosphere. At this time, both dry and wet soil conditions appear less favorable for ammonia retention in the soil (Advies beperking uitrijperiode dierlijke meststoffen, 1986).

17.5.4 Deflation Losses

Soils susceptible to deflation (wind-blown soil loss) cover approximately 82,000 ha (about 10% of the cropped area). This concerns mainly light,

sandy soils, from which strong winds may deflate up to 700 tons of topsoil in a few days (Pattje, 1948; Peerlkamp, 1971). That volume equals a layer of about 0.5 dm/ha., containing approximately 2 to 1.5 tons P_2O_5 when P-saturated (Breeuwsma, 1984), which is deposited elsewhere. The deposits of such topsoil material also contain organic matter and can affect the oxygen balance in aquatic ecosystems. Deflation depends on effective wind speed (influenced by shelter, such as hedges), soil cover, and organic-matter content of the soil. It is favored by desiccation of the topsoil, which may be a result of deeper drainage (Miedema, 1950; Spek, 1950).

17.6 Nonagricultural Water Management

Although agriculture has contributed its share to the indicated recent changes in the environment, it should be noted that its influence is as a rule far from clearly distinguishable from that of other activities that also have to do with water (e.g., water supply for industry and households, the defense of the lower parts of the country against inundation) and the distribution and availability of nutrients in the environment (e.g., discharge of household sewage, industrial wastes), either directly or indirectly. These activities and their effects vary in area and intensity. Hence it is difficult to quantify the share of each activity or sector in the effect on the national environment, the more so as various activities and factors may coincide and/or interfere.

17.7 Conclusion

The recognition of the impact of agrohydrological management and the use of manure and fertilizers on the environment has increased rapidly during the past decade. General norms for agriculture with a focus on yield and accompanied by a narrowing trend of intensification, mechanization, and enlargement of scale, need to be questioned and reconsidered. Increasing attention is being paid to the prospects of agricultural optimization and reduction of environmental impacts, in order to develop feasible alternatives that deal more specifically with agrohydrological demands (Bakel, 1986; Groenendijk, 1989) and fertilizing (e.g., Advies beperking uitrijperiode dierlijke meststoffen, 1986). This is supported by the development of hydrological systems analyses (Engelen and Jones, 1986; Gieske, 1988) and ecohydrological approaches (Wirdum, 1981; Baaijens and de Molenaar, 1982; Studiecommissie Waterbeheer Natuur, Bos en Landschap, 1989).

These developments require a broad, multidisciplinary, and interinstitutional approach, coordinated by organizations such as the NRLO (National Council for Agricultural Research) and the RMNO (Council

for Environmental and Nature Research), and by study committees, such as the COAL (Research Committee, Adjusted Agriculture) and the SWNBL (Study Committee, Water Management in relation to Nature, Forestry and Landscape Management). The SWNBL, for instance, recently produced a model for predicting the impact of water management on hydrological and hydrochemical conditions, such as groundwater levels, ion content, and acidity, by reviewing, developing, and fitting local models for the saturated and unsaturated hydrology to models for regional groundwater systems and models for surface water systems (Waterloopkundig Laboratorium, 1985a, b, 1987; Kemmers, 1986; Gieske, 1988; Groenendijk, 1989; see for survey SWNBL, 1989). In addition, the behavior of nitrogen and phosphate is modeled independent of water regime and water-dependent variables, such as acidity and oxygen availability (Mankor and Kemmers, 1987). It is evident that this broad, applied approach will have to intensify and deepen in the future, and further fundamental research must be done.

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18. Technological Changes in Energy Use in U.S. Agricultural Production

David Pimentel, Wen Dazhong, and Mario Giampietro

18.1 Introduction

Energy is equally important to land, water, and human resources in U.S. crop production. In addition to human energy, sunlight and fossil energy are the primary energy resources utilized in agricultural production. Because all technologies employed in agriculture require energy resources, the measure of energy flow in crop production provides a good indicator of the technological changes that have taken place in this sector. Energy values (kilocalories) for various resources and activities remain constant, and this is a major advantage in assessing technological change in agriculture, in contrast to economic values that are continually changing depending on the relative supply and demand of various resources and services. Another advantage of using energy as a measure of change in agricultural technology is that it can help assess the substitution of different forms of energy for various practices, as well as the substitution of land, water, and labor resources for energy.

The aim of this investigation will be to assess the changes that have occurred in U.S. agriculture during the past seventy years and examine how the new technologies have contributed to making agriculture more energy intensive. As agriculturalists, we feel that a historical analysis of the technological changes that have occurred in crop production can provide valuable insight for future agricultural policies. This is especially true if energy-use trends can be assessed in terms of future land, water,

and energy resource availability. Once energy resource use is determined and trends projected, it might be possible to assign relative price values for future energy, land, water, and human resources. Thus, together energy analyses and economic assessments can provide sound information for projecting future trends and policies.

18.2 Energy Resources

The use of fossil fuels in U.S. agriculture and society as a whole is a recent event that did not grow rapidly until after 1900 (Table 18.1). As recently as 1850, the primary energy resources for society were fuelwood and human labor (Executive Office of the President, EOP, 1977). Today the United States consumes 19×10^{15} kcal (71 quads) (Dept. of Energy [DOE], 1983). On a per capita basis, this is equivalent to 2,500 gal (9,480 l) of oil per person per year.

About 17% of the total energy used in the U.S. economy is consumed in the food systems (Pimentel, 1984a). About 6% is for production, 6% for processing and packaging, and the remaining 5% is for distribution and preparation.

This 17% of total U.S. energy represents about 1,500 liters (400 gal) of fuel per person annually just for food. It has been calculated that if a world population of 4.7 billion humans ate as we do in the United States and used our agricultural technology, the total known reserves of oil on earth would last a mere 12 years (Pimentel, 1984b). This is using all known oil reserves only for food, none for transportation, heating, and cooling. This clearly illustrates the limitations of fossil fuel resources relative to the food needs of a rapidly growing world population.

Since the oil crisis in 1973, the quantity of energy used in U.S. crop production has continued to rise (Tables 18.1 and 18.2). At the same time, the on-farm work force has continued to decline (USDA, 1982a). Some agriculturalists proudly point to the fact that only about 3% of the work force is involved in direct farming and thus are feeding the rest of the U.S. population (USDA, 1982a). However, this is a misleading statistic because the farmer hardly feeds himself entirely and he goes to the same supermarket that we do to purchase food. He depends upon Detroit for his tractors and other farm machinery equipment, he depends upon the oil industry to fuel his tractors and other implements, he must rely upon the petrochemical industry to provide the thousands of different chemicals that he uses; in addition, many other resources are supplied to his farm by various industries. After the crops and livestock are harvested on the farm, the farmer relies upon the transport and food-processing sectors to move and process these foods. Eventually, the foods are shipped to wholesalers and are handled by food retailers. Thus, for every farm worker, it is estimated there are two to three farm-support

Table 18.1. Quantities of various inputs to produce corn using only labor, draft animals, and mechanization from 1910 to 1985

	Hand-produced										
Years	1910	1920	1945	1950	1954	1959	1964	1970	1975	1980	1985
Labor (hours/ha)	1,200 ^a	120 ^b	57 ^f	44 ^f	42 ^f	35 ^g	27 ^g	22 ^g	17 ^h	12 ^h	10 ^d
Machinery (kg/ha)	1 ^c	15 ^b	22 ^g	30 ^g	35 ^g	42 ^g	49 ^g	49 ^g	50 ^h	55 ^h	55 ^d
Draft animals (h/ha)	0	120 ^b	ND	ND	ND	ND	ND	ND	ND	ND	ND
Fuel (l/ha)	ND	ND	120 ⁱ	135 ⁱ	150 ⁱ	155 ⁱ	125 ⁱ	120 ⁱ	60 ^h	50 ^h	40 ^d
Gasoline	ND	ND	20 ⁱ	25 ⁱ	30 ⁱ	35 ⁱ	65 ⁱ	80 ⁱ	70 ^h	75 ^h	75 ^d
Diesel	ND	ND	3,000 ⁿ	2,000 ⁿ	1,000 ⁿ	1,000 ⁿ	1,000 ⁿ	1,000 ⁿ	1,000 ⁿ	1,000 ⁿ	1,000 ⁿ
Manure	ND	4,000 ⁿ	0	8 ^e	30 ^g	46 ^g	55 ^j	118 ^j	111 ^j	140 ^j	152 ^j
N (kg/ha)	0	0	0	17 ^g	30 ^g	46 ^g	55 ^j	118 ^j	111 ^j	140 ^j	152 ^j
P (kg/ha)	0	0	0	8 ^e	13 ^g	18 ^g	36 ^j	72 ^j	56 ^j	65 ^j	58 ^j
K (kg/ha)	0	0	0	11 ^g	20 ^g	34 ^g	28 ^j	68 ^j	62 ^j	78 ^j	75 ^j
Lime (kg/ha)	0	10 ^d	145 ^c	195 ^c	124 ^c	158 ^c	203 ^c	220 ^c	220 ^h	426 ^k	426 ^d
Seeds (kg/ha)	11 ^d	11 ^d	11 ^d	13 ^g	17 ^g	19 ^g	21 ^g	21 ^g	21 ^h	21 ^h	21 ^d
Insecticides (kg/ha)	0	0	0	0.1 ^g	0.2 ^d	0.3 ^d	0.4 ^d	0.4 ^v	0.5 ^v	0.6 ^v	0.6 ^d
Herbicides (kg/ha)	0	0	0	0.05 ^g	0.1 ^g	0.3 ^g	0.4 ^g	2 ^v	3 ^v	3 ^v	3.5 ^d
Irrigation (%/ha)	0	0	0	1 ⁱ	2 ^o	3 ^o	5 ^p	9 ^q	16 ^r	17 ^s	18 ^s
Drying (kg/ha)	ND	ND	1 ⁱ	1 ⁱ	2 ^o	3 ^o	5 ^p	9 ^q	16 ^r	17 ^s	18 ^s
Electricity (10 ³ kcal)	0	0	43 ^d	48 ^d	77 ^d	271 ^d	725 ^d	1,880 ^e	2,290 ^d	3,200 ^d	3,800 ^d
Transport (kg/ha)	0	ND	8 ^d	16 ^d	24 ^d	36 ^d	60 ^d	80 ^d	90 ^d	100 ^d	100 ^d
Yield (kg/ha)	ND	25 ^m	170 ^m	210 ^m	262 ^m	287 ^m	325 ^m	305 ^m	298 ^m	326 ^m	322 ^m
	1,880 ^e	1,880 ^e	2,132 ^g	2,383 ^g	2,572 ^g	3,387 ^g	4,265 ^g	5,080 ^g	5,143 ⁱ	6,500 ⁱ	7,400 ^u

ND = no data; value > 0 but no data exist. ^aEstimated from Lewis, 1951. ^bEstimated from Pimentel, 1984c. ^cPimentel and Pimentel, 1979. ^dEstimated. ^eUSDA, 1970. ^fUSDA, 1954. ^gPimentel et al., 1973. ^hPimentel and Burgess, 1980. ⁱQuantities from Pimentel et al. (1973) and proportions estimated. ^jUSDA, 1987. ^kUSDA, 1981. ^lPercentage of corn acreage irrigated (USBC, 1952). ^mTransport of machinery, fuel, and nitrogen fertilizer. ⁿEstimated amount of livestock manure containing 80% moisture. ^oPercentage of corn acreage irrigated (USBC, 1962). ^pPercentage of corn acreage irrigated (USBC, 1967). ^qPercentage of corn acreage irrigated (USBC, 1973). ^rPercentage of corn acreage irrigated (FEA, 1976). ^sEstimated percentage of corn acreage irrigated. ^tThree-year running average yield (USDA, 1976; USDA, 1982a). ^uUSDA, 1986. ^vUSDA, 1982c.

Table 18.2. The energy input for various items used in corn production from 1700 to 1985 (thousands kcal/hectare)

Years	1700	1910	1920	1945	1950	1954	1959	1964	1970	1975	1980	1985
Labor ^a	653	65	65	31	24	23	19	15	12	10	7	6
Machinery ^b	19	278	278	407	555	648	777	907	907	925	1,018	1,018
Draft animals ^c	0	886	886	0	0	0	0	0	0	0	0	0
Fuel ^c												
Gasoline	0	0	0	1,200	1,350	1,500	1,550	1,250	1,200	600	500	400
Diesel	0	0	0	228	275	342	399	741	912	912	878	878
Manure ^e	0	0	0	0	0	0	0	0	0	0	0	0
N ^r	0	0	0	168	357	630	966	1,555	2,478	2,331	2,940	3,192
P ^s	0	0	0	50	69	82	113	227	454	353	409	365
K ^h	0	0	0	15	28	50	85	70	170	155	195	187
Lime ⁱ	0	3	3	46	61	39	50	64	69	69	134	134
Seeds ^j	44	44	44	161	322	421	470	520	520	520	520	520
Insecticides ^k	0	0	0	0	7	13	20	27	40	50	60	60
Herbicides ^l	0	0	0	0	3	7	20	40	200	300	300	350
Irrigation ^m	0	ND	ND	125	125	250	375	625	1,125	2,000	2,125	2,250
Drying ⁿ	0	0	0	9	10	15	54	145	376	458	640	760
Electricity ^o	ND	ND	1	8	16	24	36	60	80	90	100	100
Transport ^p	ND	25	25	44	58	67	79	89	84	82	90	89
Total	716	1,301	1,302	2,492	3,260	4,111	5,013	5,935	8,627	8,855	9,916	10,309
Ratio	10.5	5.8	5.8	3.4	2.9	2.5	2.7	2.9	2.4	2.3	2.6	2.9
Yield	7,520	7,520	7,520	8,528	9,532	10,288	13,548	17,060	20,320	20,575	26,000	29,600

Table 18.2 (continued)

ND = no data; value > 0 but no data exist. ^aFood energy consumed per laborer per day was assumed to be 3,110 kcal from 1700 to 1970, 3,300 kcal for 1975, and 3,500 kcal for 1980 to 1983. ^bThe energy input per kilogram of steel in tools and other machinery was 18,500 kcal (Doering, 1980). ^cThe food energy per hour of draft animal use was calculated to be 7,380 kcal (Pimentel, 1984c). ^dA liter of gasoline and diesel fuel was calculated to contain 10,000 and 11,400 kcal (Cervinka, 1980). These values include the energy input for mining and refining. ^eNo charge was made for the manure input. This input was assumed to be included in either the draft animal input or the machinery and fuel inputs. ^fNitrogen = 21,000 kcal/kg (Dovring and McDowell, 1980). ^gPhosphorus = 6,300 kcal/kg (Dovring and McDowell, 1980). ^hPotassium = 2,500 kcal/kg (Dovring and McDowell, 1980). ⁱLimestone = 315 kcal/kg (Terhune, 1980). ^jFrom 1700 to 1920, it was assumed that each kilogram of corn equaled 4,000 kcal, whereas when hybrid seed was used from 1945 to 1985 the cost was 24,750 kcal/kg (Heichel, 1980). ^kChlorinated insecticides dominated use from 1945 to 1964 and the energy input was calculated to be 67,000 kcal whereas from 1970 to 1985 carbamate and phosphate dominated use and the energy input for these was calculated to be 100,000 kcal/kg (Pimentel, 1980). ^lPhenoxy herbicides dominated use from 1945 to 1959 and the energy input for these are calculated to be 67,000 kcal/kg whereas from 1964 to 1985 other types of herbicides dominated use and the energy input for these are calculated to be 100,000 kcal/kg (Pimentel, 1980). ^mWater used per irrigated hectare was assumed to be 37.5 cm from 1945 to 1970 and 45 cm from 1974 to 1983. The percentage of corn acreage receiving irrigation are shown in Table 18.1. The energy required per kilogram of irrigation water pumped from a depth of 100 meters was calculated to be 300,000 kcal/cm. ⁿThe quantity of corn per hectare that required drying is shown on Table 18.1. The energy required per kilogram dried was 200 kcal (Peart et al., 1980). ^oIncludes energy input required to produce the electricity. ^pFor the goods transported to the farm, an input of 275 kcal/kg was included (Pimentel, 1980).

workers. If the total work force in the food systems is considered, then about 20% of the U.S. work force is involved in supplying food (Pimentel et al., 1973).

Interestingly, about 20% of the work force was involved in the food system in the United States in the 1920s. The primary difference today is that only a small portion of the work force is located on the farm.

18.3 Energy Inputs in Corn Production

18.3.1 Corn Yields

U.S. corn yields remained relatively static at about 1,880 kg/ha (about 30 bu/acre) from 1909 to 1940 (Figure 18.1). It was not until about 1945 that corn yields started to increase. At about the same time, we started using hybrid corn varieties, applying commercial fertilizers and pesticides, and employing other new energy-intensive technologies (Pimentel et al., 1973).

From 1945 to 1983, corn yields increased about 3-fold (Figure 18.1). Concurrently, total energy input has increased about 4-fold (Tables 18.1 and 18.2). The technological changes that have taken place in agriculture during the past 73 years are examined below.

18.3.2 Labor

To raise corn by manpower alone requires about 1,200 hours of labor per hectare per season (Pimentel and Pimentel, 1979) (Table 18.1). Early native Americans and perhaps a few early European settlers raised corn by hand, but starting with U.S. independence, most corn culture involved draft animal power using both oxen and horses.

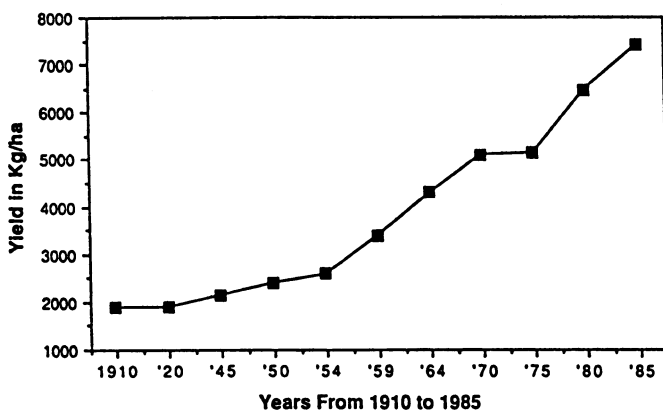


Figure 18.1. U.S. corn yields from 1910 to 1985 (from Table 18.1).

The use of 200 h of oxen power to produce a hectare of corn reduces the manpower input from 1,200 h for hand-produced corn to about 400 h (Pimentel and Pimentel, 1979). Thus, each hour of oxen input replaced 4 h of manpower input. It has been estimated that the effective use of about 120 h of horsepower could reduce the labor input for corn production to about 120 h, or 1 h of horse power replaces about 10 h of manpower (Pimentel, 1984c). Horsepower dominated U.S. corn production between 1910 and 1920 (Tables 18.1 and 18.2).

Today, with the heavy mechanization of agriculture, the labor input in corn production has been reduced to about 10 h/ha (Tables 18.1 and 18.2). However, we must note that because of this technological change, human labor is no longer related to direct power delivery. This is about $\frac{1}{120}$ th of the input required to produce corn by hand; however, this does not take into account, as mentioned, all the indirect labor inputs that go into agricultural production. If the indirect labor input is taken into consideration, then current U.S. corn production uses about $\frac{1}{40}$ th to $\frac{1}{50}$ th of the labor input for hand-grown corn. This is still a dramatic reduction in the total amount of human activity required to produce corn over the past few decades.

18.3.3 Machinery and Power

Engine power has made a tremendous difference in U.S. society as well as elsewhere in the world. This can be illustrated by analyzing the manpower equivalent present in a gallon of fuel. One gallon (3.79 l) of fuel fed to a small gasoline engine will provide 20% of the heat energy produced in the form of power. Thus, from about 31,000 kcal in a gallon of fuel, about 7.2 kwh can be produced, which is equivalent of about 10 hp/h or 100 mph of power (Pimentel and Pimentel, 1979). Thus, 1 gal of gasoline can provide about 2.5 weeks of human work equivalents. This is part of the reason for the dramatic reduction in labor inputs from 57 h/ha to only 10 h/ha that occurred in on-farm corn production in the United States from 1945 to the present (Table 18.1).

Interestingly, the total amount of fuel consumed has declined from about 140 l/ha in 1945 to about 115 l/ha today (Table 18.1). The reasons for the decline have been improved engines, changes from gasoline to diesel fuel, and larger farm machinery. The weight of the machinery per labor hour, for example, has grown from about 0.4 kg in 1945 to about 5.5 kg/h in 1983—about a 14-fold increase (Table 18.1). Hence, where liquid fuel inputs have declined, fossil energy inputs for machinery have risen dramatically.

Initially in corn production, the principal fuel used in tractors was 85% gasoline and only 15% diesel fuel (Table 18.1). With time, there was a shift toward diesel fuel, and today at least 65% of tractor fuel is diesel fuel (Table 18.1). Diesel fuel has advantages because it can provide 20

to 25% more power or greater efficiency per unit of fossil energy (Council for Agricultural Science and Technology [CAST], 1975).

This is part of the reason for the decline in total fuel use. Another reason for the reduced fuel consumption per hectare has been the use of large farm equipment that allows more operations to be performed over less time. The result is less fuel consumed per hectare in corn production.

18.3.4 Fertilizers

Early hand-produced crops depended upon the nutrients that accumulated in the soil and wild vegetation growing on the uncultivated land. For example, in early slash/burn agriculture, vegetation was cut and burned to release the nutrients to the soil for crop production. Usually the land had to lay fallow for about 20 years before sufficient nutrients would accumulate in the soil and vegetation. The land could then be tilled and planted to crops for 2 years out of 22 years.

Early U.S. agriculture was primarily organically based; that is, nutrients for crop production were provided mostly by livestock manure and green manures. In most cases, the farming system required 2 ha of land to produce 1 ha of a crop. For example, 1 ha would be planted to a legume such as clover or vetch, and the following year this legume would be plowed under and planted to corn. This 2-year rotation system did provide an adequate amount of nitrogen for the corn crop each year; however, the soils were slowly being depleted of phosphorus, potassium, and calcium.

In 1945, only 8 kg/ha of nitrogen and phosphorus and 6 kg/ha of potassium were applied (Figure 18.2). By 1983, nitrogen application rates had reached a high of 152 kg/ha. This was nearly a 20-fold increase in application rates from 1945 to 1983.

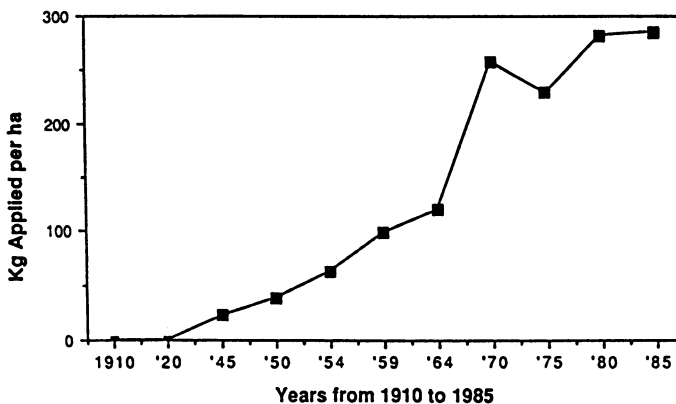


Figure 18.2. Chemical fertilizer (nitrogen, N; phosphorus, P; and potassium, K) applied per ha in corn production (from Table 18.1).

Note that the energy inputs for nitrogen alone in 1983 were greater than the total energy inputs for all items used in corn production in 1945 (Table 18.2). This is a clear example of how U.S. agricultural technologies have changed from 1945 to 1983.

During this 38-year period there was a reported 30% improvement in efficiency of producing nitrogen fertilizer (Smil et al., 1983); however, these improved efficiencies have been offset by uses of new, larger, and more complicated equipment (Dovring and McDowell, 1984).

Although the amounts of phosphorus and potassium applied per hectare rose significantly from 1945 to 1983, these quantities clearly did not grow as rapidly as occurred with nitrogen, and both potassium and phosphorus require significantly less energy per kilogram to produce (Table 18.2).

The quantities of lime applied to agricultural land also rose about 3-fold from 1945 to 1983, but lime is the least energy costly of the fertilizers that are used in corn production (Table 18.2).

18.3.5 Pesticides

Little or no pesticide was used in corn production in 1945 (Table 18.1). The quantity of insecticide applied to corn rose from 0.1 kg/ha in 1950 to 3 kg/ha by 1983. The insecticides used in the early 1950s and 1960s were primarily chlorinated insecticides. Starting with the ban of some chlorinated insecticides in the early 1970s, there was a gradual shift from the chlorinated insecticides to carbamate and phosphate insecticides. With this change in the chemical makeup of insecticides, the energy inputs per kilogram of pesticide produced increased about 50%, and the total inputs for chemical insect control rose 45-fold (Table 18.2).

Changes in herbicide use also occurred in corn production starting in 1950. The first herbicide used in corn production was 2,4-D, a phenoxy herbicide that was relatively efficient to produce in terms of energy input per kilogram. The newer triazines and other herbicides that were added during the 1960s and later, were 50% more energy costly to produce (Table 18.2). The total input for chemical weed control increased 267-fold from 1950 to date. Hence, changes occur not only in the quantities of pesticides applied, but in the kinds of insecticides and herbicides used.

18.3.6 Irrigation

The application of irrigation water for corn production has increased steadily over the years. Irrigation of corn acreage has increased from less than 1% in 1945 (Tables 18.1 and 18.2) to an estimated 18% today. Water applied per irrigated hectare has increased from 1.8 million l to slightly more than 2.2 million l today. The energy input for irrigation water during the period 1945 to 1983 rose nearly 20-fold (Table 18.2).

18.3.7 Drying

Another major change in corn production technology during the last 38 years has been in the way corn is harvested. Initially, corn was harvested as corn on the cob. But gradually, more and more corn has been harvested as grain directly in the field, and today, most corn is harvested as grain. Of course, when corn is harvested directly as grain, it contains 25 to 30% moisture. This corn must be dried and must not contain more than 13 to 15% moisture before being placed in storage. About 200 kcal of energy are required to dry 1 kg of corn (Table 18.1 and 18.2).

Harvesting corn on the cob and then drying it in corn cribs has been calculated to use 33% less fossil energy than harvesting the corn as grain and then drying it using fossil energy (Hudson, 1984). The corn on the cob in the crib is dried by the wind or solar energy.

18.3.8 Electricity

Electricity is used for a variety of purposes on farms including moving goods in and out of storage, running fans, and operating other pieces of equipment. The energy input for electricity given in the calculations in Table 18.2 includes the total energy required to produce the electricity. About 3 kcal of coal, for example, is required to produce 1 kcal of electricity (Pimentel et al., 1984a).

Note, the energy for electricity would be much higher if that used by the farm family were included (Pimentel et al., 1973).

18.3.9 Transport

Transportation costs were relatively small because only machinery, fuel, and nitrogen fertilizer transport costs had to be calculated; the transport costs for the other items had already been included. Note, overall energy inputs for transportation more than doubled from 1945 to 1983, confirming the intensiveness of agricultural management over this period (Table 18.2).

18.4 Trends in Energy Use in U.S. Agriculture

Energy inputs in corn production have continued to increase from hand and draft animal power systems to the highly mechanized systems of today (Table 18.2). Only an estimated 716,000 kcal were used to produce 1 ha of corn by hand in 1700, whereas 11.0 million kcal are employed in U.S. corn production today. This represents a 15-fold increase in energy inputs. Yields during this period have grown 3.5-fold (Tables 18.1 and 18.2).

The energy crisis that struck the United States in 1973 has apparently not slowed the growth of energy use in corn production (Table 18.2). These data suggest that an estimated 18% rise in fossil energy inputs in U.S. corn production occurred from 1975 to 1983. Grain yields during the same period rose 26% (Tables 18.1 and 18.2).

The 26% increase in yield associated with a 18% rise in energy use suggests that some improvement in corn production technologies has occurred during the last 10 years. In fact, there have been several improvements. For example, less total liquid fuel is now used in farm machinery (Tables 18.1 and 18.2). This reduction, as mentioned, was due in part to a change from gasoline to diesel fuel and to using larger farm equipment. At the same time, farmers were probably taking better care of the operation of their machinery, including restricting the use of farm equipment to only essential tasks.

Fertilizers have also been utilized more effectively. For example, more nitrogen fertilizer is probably being applied today, during the growing season when the crops can use the nitrogen, than previously. During the early 1970s, some nitrogen was applied to corn fields during the winter months when farm labor and machinery were generally idle. Of course, some of this nitrogen was wasted because it leached into the groundwater and streams. Nitrogen is a serious pollutant of both groundwater and streams in some parts of the nation today (Council on Environmental Quality [CEQ], 1978).

The energy output in the form of grain per kcal of energy input has generally declined with time (Table 18.2). For example, producing corn by hand was calculated to provide 11 kcal of corn per kcal of input. For draft animal power, the ratio was 6:1 and for the highly mechanized system of 1983, the ratio is calculated to be 2.4:1 (Table 18.2).

These results emphasize the efficiency of human power in crop production when provided with simple tools compared with the highly mechanized system of 1983 (Table 18.2). However, in terms of economic inputs and outputs, the highly mechanized system is more profitable because today, power generated by human muscle is significantly more expensive than power generated by thermic engines using fossil fuel.

How do solar energy inputs relate to the use of fossil energy use in corn production? The solar energy reaching 1 ha during the year averages about 14×10^9 kcal (Reifsnyder and Lull, 1965). During an average 4-month summer growing season in the temperate region, nearly 7×10^9 kcal reach 1 ha. With a corn grain yield of 6,500 kg/ha plus another 6,500 kg/ha in stover biomass, the energy in the corn represents about 0.4% of the solar energy captured. For the corn grain the percentage is only 0.2% or an input of about 56 kcal of solar energy per kcal of corn grain produced.

Note that the corn produced by hand labor is less than half as efficient in converting solar energy into corn grain as that produced by mecha-

nization in 1983; about 0.1% of the solar energy is converted into corn grain in the hand-produced system listed in Tables 18.1 and 18.2. Hence, about 93 kcal of solar energy input are required to produce 1 kcal of corn in the hand-produced system.

In summary, the highly mechanized corn production system was more efficient in collecting solar energy and converting it into corn grain than the hand-produced system. This is true even if the fossil fuel inputs are included in the analysis.

18.5 Alternatives for Improving Energy Efficiency in U.S. Corn Production

18.5.1 Labor

It has been estimated that the yields of corn could be maintained while reducing the fossil energy inputs by nearly one-half (Pimentel et al., 1973; Pimentel and Pimentel, 1979). This would require, however, significant inputs of labor. Labor with simple tools can perform most agricultural tasks more efficiently than most large machines. The high cost of labor today compared with fuel, however, would generally discourage this trend. A gallon of diesel fuel provides about 100 mph of power at a cost of about \$1.25 for the fuel. The equivalent in human power calculated at today's minimum wage would cost \$335. Thus, oil will provide the same amount of power as human labor for $\frac{1}{268}$ th the cost.

Today, corn is produced with an input of about 10 h/ha. It is doubtful that many farmers will find it profitable in the near future to reduce the labor input much further. At the same time it is unlikely that farmers will attempt to replace machinery and fuel input with increased labor in the future.

18.5.2 Machinery and Fuel

Selecting pieces of equipment of the right size for various agricultural tasks may improve efficiency and conserve fuel. The substitution of diesel engines for gasoline engines will provide 20 to 25% increased efficiency per liter of fuel consumed (CAST, 1975). Another important factor in tractor efficiency is careful maintenance of the engines and operating the machinery at optimum speeds in carrying out various tasks.

Although the use of larger machinery may conserve energy in some crop production tasks, large machinery requires additional energy because of the environmental damage this equipment causes. For example, the use of some large machinery causes increased soil erosion and thus loss of soil nutrients. In some situations, the large pieces of machinery cannot follow contours on sloping fields, and thus soil erosion is increased (Office of Technology Assessment, [OTA], 1982). In other situations, terraces

have been tilled and destroyed because the machinery was too wide for the terraces, and again erosion increased (OTA, 1982). Hence, whether the large machinery is actually saving fuel depends on the increase in soil erosion and loss of nutrients that results from its use. This problem should be assessed.

Some have suggested that corn residues and/or corn grain could be effectively used to produce ethanol for use in tractors. However, the environmental and social costs of producing ethanol are much too high for this system to provide any net return in terms of either energy or economics (Pimentel et al., 1984b). Ethanol production using crop and/or corn grain generally results in net loss of energy plus environmental degradation over time.

18.5.3 Fertilizers

Some improvements in fertilizer use (especially nitrogen) have occurred already, but many more possibilities exist. In particular, more efficient fertilizer application technologies are needed. These technologies would help maintain corn yields while actually reducing the quantity of fertilizer applied to the land.

Other means of reducing commercial fertilizer use would be to make more effective use of livestock manure. About one-half of the nitrogen (N), phosphorus (P), and potassium (K) in livestock manure are currently lost due to poor management (Muck, 1982). Instead of spreading livestock manure directly on the field during winter and other noncrop growing periods as is the current practice, the manure would have to be stored in plastic-lined ponds. The stored manure would then be applied to the land just before planting and covered by soil immediately to trap the nitrogen in the soil. Clearly, applying manure in the spring would increase the need for labor during the busy spring planting period.

Despite this trade-off, the amount of nitrogen available to crop production could be greatly increased by effective handling of manure. Currently about 4 million tons of nitrogen are applied to U.S. land as livestock manure. This calculation is based on the assumption that 90% of all manure ends up on the agricultural land (Energy Research Advisory Board [ERAB], 1981; Pimentel, 1984a). Only about one-third of the manure produced is actually collected in barns and pens; hence, about 1.5 million tons might potentially be available for application to cropland. Effective use of this 1.5 million tons of nitrogen by good management would help reduce dependence on the estimated 10.2 million tons of commercial nitrogen that is now applied to U.S. crops (USDA, 1982a).

An estimated 10% of the manure produced by livestock is not being applied to the land because of distance. Because manure contains 70 to 90% water, it cannot be transported very far before the energy used in transportation will outweigh the energy contained in the N, P, and K nutrients (Pimentel et al., 1983).

Some technologies are being perfected whereby legumes can be grown between corn rows to supply nitrogen to the crop (Scott, 1982). The legume is seeded between the corn during late July, when the growth of the legume will no longer interfere with corn production. If the legume is allowed to grow during the fall and early spring before being plowed under, an estimated 130 kg/ha of nitrogen may be produced by the legumes. In addition to providing large quantities of nitrogen, this system helps protect the soil from erosion.

The legume system, however, has two disadvantages: first, the legume must be planted during the summer months and this of course requires inputs of labor and legume seed. Also, the soil cannot be tilled in the fall but has to be tilled during the spring when the farmer is extremely busy with other planting tasks.

18.5.4 Insecticides

Most of the insecticide used in corn production today is for corn root-worm control (Pimentel et al., 1977). This insecticide use could be eliminated by planting corn in rotation following either a legume, such as soybeans, or a small grain like wheat. The cost of this technology is the use of a substitute crop that may not return the same profit per hectare that corn does.

18.5.5 Herbicides

Corn uses more herbicide than any other single crop in the nation (Eichers, 1981). An estimated 8 kg/ha of herbicide was applied in 1983 (Table 18.1). Some of the increased use of herbicide is due to the use of no-till technology in corn production.

The popular literature claims that no-till corn production saves energy. No-till culture does require less tractor fuel for tilling the soil, but it also requires 2 to 4 times more energy for pest control. Leaving corn residues on the land surface, for example, does not destroy the pests in the corn residues as occurs when they are buried. Thus, insect and plant pathogen problems are more severe in no-till corn, including organisms that attack the seeds. The cold/wet conditions in no-till soil result in a loss of about one-third of the corn seed, thus about one-third more seed has to be planted to achieve a good corn stand. Hybrid corn seed is also costly in terms of energy (24,750 kcal/kg) input (Heichel, 1980).

In addition to the insect and plant pathogen problems in no-till corn, slugs and mice often become problems and have to be controlled. Pesticides to control these pests add to the costs. However, no-till has two major advantages: it saves labor and it is especially effective in reducing soil erosion. Erosion losses may be reduced by 10% to 100% (USDA, 1975).

18.5.6 Drying

Earlier it was mentioned that harvesting corn on the cob requires one-third less energy than harvesting the corn as grain. In addition to this advantage, this technology could help provide a biomass energy source (cobs). The corn cobs can also be ground and combined with corn as a concentrated feed for cattle. Corn cobs also make a good fuel.

18.5.7 Electricity and Transport

Few alternatives exist that would help reduce electricity use on the farm. For transportation, if more goods were transported by rail instead of trucks, significant energy savings would be possible. Per ton of goods transported by rail, the energy required is only 0.12 kcal/km compared to truck transport, which requires 0.83 kcal/km (Pimentel and Pimentel, 1979). Thus, rail transport is 7-fold more efficient than truck transport.

18.5.8 Conclusion

During the past 75 years, there have been a great many changes in U.S. agricultural technology. A major change has been the substitution of fossil energy for labor, draft animals, land, water, nutrients, pest control, and environmental degradation. Because of these changes, fossil energy use has increased more than 100-fold during the past 75 years.

The increase in the intensity of energy use, especially of fossil-fuel-based sources of energy, makes U.S. agriculture much more vulnerable to fluctuations in world oil prices and supplies. An understanding of energy resource use can aid in the search for a means of evaluating current agricultural practices, contributing at the same time to the development of policies that establish a more sustainable basis for our food production systems.

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19. Energy Flow in Agroecosystems of Northeast China

Wen Dazhong and David Pimentel

19.1 Introduction

During the past three decades, agriculture in China has changed dramatically. Agricultural production units of individual peasant families of the 1950s were replaced by collective production organizations or people's communes; and fossil fuel energy inputs in the form of synthetic fertilizers, pesticides, and machinery were used to increase agricultural production. In fact, the total amount of fossil fuel used in Chinese agriculture rose from 7×10^{12} kcal in 1957 to 681×10^{12} kcal in 1978, nearly a 100-fold increase (Taylor, 1981; Lu, 1982). Grain production in China at the same time rose from 113.2 million tons in 1949 to 332.4 million tons in 1979—about a 3-fold increase (Agricultural Almanac of China (AAC), 1980). Thus, a 100-fold increase in fossil fuel use has resulted in a 3-fold rise in total grain production in China.

During the period from 1950 to 1978, most of the traditional organic agroecosystems that had been dominant in China disappeared. Although fossil energy use rose 100-fold, and agriculture became more energy intensive, not all the traditional organic technologies employed in agriculture have been replaced. In fact, most of the current agricultural systems in China employ a combination of human, draft animal, and tractor power and a combination of both organic and commercial fertilizers.

During this same period, more than 1,000 energy-intensive, mechanized state-administered grain farms have been established in some of

the marginal land areas of China (AAC, 1980). Although the state farms are much more energy intensive than the collective agricultural production units of the people's communes, the level of mechanization and energy intensiveness is still much lower than in the West.

A clear need exists to increase both food and biomass fuel production to meet the demands of the growing numbers of people in China. Increasing food and biomass fuel will require making better use of land, water, and energy resources for agricultural and forestry production. To help identify technologies of the future that might aid in improving resource use and increasing food and biomass fuel supplies, we have made an analysis of the changes in agricultural and forestry practices that have occurred. Our aim is to document which of these has contributed the most to increasing food and biomass yields. For this analysis, comparisons will be made of food and biomass fuel production systems of early organic, the people's communes, and the state farms. Though the forms of agricultural production organization have changed dramatically since 1980, this analysis will be useful in making future strategies for agricultural development in China.

19.2 Energy Flows in Agroecosystems of People's Communes

Most agricultural products in northeast China were produced by people's communes or agricultural collectives before 1980. The data for this assessment came from the Hailun Statistics Bureau of Hailun county, located in the center of Heilongjiang province. Data were taken from a 3-year period (1976 to 78) to reduce the influence of annual climatic fluctuations (Tian, 1978). Information from twenty-eight agricultural communes was utilized in the analysis.

Hailun county commune agroecosystem covered 322,000 ha, of which 284,270 ha were in cropland, 21,330 ha in grassland, and 16,400 ha in woodland. In the crop system, an average 3.8 million kcal/ha of energy was invested to produce food (Table 19.1). About 24% of this total was fossil energy and the remainder was renewable energy. The major inputs of fossil energy were for diesel fuel and nitrogen (N) fertilizer, and these two inputs accounted for more than three-quarters of the fossil energy inputs.

For the renewable energy, the major inputs were for manure, crop residues, seeds, human power, and horse power (Table 19.1). Human labor averaged 958 hr/ha and draft horse labor 291 hr/ha. Although most of the seeds were hybrid types, they were produced by the communes themselves. Both human and animal wastes were utilized as a source of fertilizer. An average of 263 kg/ha (dry) of manure was used, plus 288 kg/ha (dry) of composted crop residues were returned to the land. The 288 kg of residue accounts for only 12% of the total harvested crop res-

Table 19.1. Energy inputs and outputs per hectare for crop production in traditional organic, commune, and state-farm systems in Hailun County

Items	System					
	Traditional Organic (1952-1954)		Commune (1976-1978)		State-Farm (1976-1978)	
	Quantity	kcal	Quantity	kcal	Quantity	kcal
Labor ^a	1,060 hr	190,868	958 hr	172,404	608 hr	109,390
Horses ^b	422 hr	1,012,560	291 hr	698,400	99 hr	237,600
Tools and animal draft equipment ^c	2.4 kg	49,295	1.9 kg	39,353	0.4 kg	8,738
Machinery ^d			3.4 kg	61,200	14.5 kg	251,436
Gasoline ^e	0	0	2.1 l	20,840	31.2 l	315,536
Diesel ^f	0	0	53.0 l	605,333	142.5 l	1,626,817
Electricity ^g	0	0	11.0 kwh	31,379	65.0 kwh	186,249
Nitrogen ^h	0	0	10.0 kg	120,181	28.0 kg	335,871
Phosphorus ⁱ	0	0	0.2 kg	657	13.8 kg	41,418
Pesticide ^j	0	0	0.01 kg	869	0.015 kg	1,326
Repair parts and goods ^k	0	0	6.0 yuans	27,561	44.5 yuans	205,702
Transportation ^l	0	0	51.9 kg	13,335	158.9 kg	40,832
Seeds ^m	46.5 kg	176,317	91.1 kg	345,620	180.7 kg	738,510
Manure ⁿ	269 kg	1,209,370	263.0 kg	1,183,700	133.0 kg	598,384
Harvested residue returned to land ^o	385 kg	1,443,525	288.0 kg	1,092,909	345.0 kg	1,309,066
Total input		4,081,935		4,413,748		6,006,875
Crop yield (output)		5,276,838		5,970,169		6,816,697
Crop output/total energy input		1.29		1.35		1.13
Crop output/fossil fuel energy input		107.0		6.48		2.26

Table 19.1 (continued)

- ^aData for traditional organic system from Dazhong and Pimentel (1984a). A male worker had 300 working days per year and 8 hours each day, and a female worker had 150 working days per year and 8 hours each day. The energy equivalent per human hour input was calculated to be 180 kcal (Norman, 1978).
- ^bData for traditional organic system from Dazhong and Pimentel (1984a). It was calculated that each horse worked for 1,600 hours per year. The energy equivalent per horse-hour of work was calculated to be 2,400 kcal/hr (Cox and Atkins, 1979).
- ^cData for traditional organic system from Dazhong and Pimentel (1984a). Energy equivalent of these tools and implements was 20,712 kcal/kg (Pimentel, 1976).
- ^dEnergy equivalent of machinery was 18,000 kcal/kg (Doering, 1980).
- ^eEnergy equivalent of gasoline was 10,109 kcal/l (Cervinka, 1980).
- ^fEnergy equivalent of diesel was 11,414 kcal/l (Cervinka, 1980).
- ^gEnergy equivalent of electricity was 2,863 kcal/kwh (Cervinka, 1980).
- ^hEnergy equivalent of nitrogen was 12,000 kcal/kg (Lockeretz, 1980).
- ⁱEnergy equivalent of phosphorus was 3,000 kcal/kg (Lockeretz, 1980).
- ^jEnergy equivalent of pesticides was 86,910 kcal/kg (Lockeretz, 1980).
- ^kEnergy consumption per unit output value on average in China in 1973 was 4,620 kcal/yuan (Chinese currency) (Ma and Shun, 1981).
- ^lIncluded fuel and machinery. Energy equivalent of transportation is 257 kcal/kg (Pimentel, 1980b).
- ^mData for traditional organic system from Dazhong and Pimentel (1984a). Estimated on the basis of statistics of seed requirement and seed energy content for each crop.
- ⁿData for traditional organic system from Dazhong and Pimentel (1984a). Assuming that manure (dry) produced per individual per year was: human = 40 kg; pig = 113 kg; horse and ox = 1,205 kg; sheep = 150 kg; and poultry = 4 kg. The energy equivalent of manure was 4,500 kcal/kg (Beijingshi Nonlinju, 1980; Shiziang Nongkeyuan, 1975). Only half of the manure was assumed to be returned to the crop field (Zhang, 1978).
- ^oData for traditional organic system from Dazhong and Pimentel (1984a). We estimated that all potato residue and soybean residue were directly returned to the field and about 5% of other harvested crop residues were returned to the field after being composted.

Table 19.2. Crops and crop residues harvested in early traditional organic system, commune system, and state farm system in Hailun County

	System											
	Traditional Organic (1952-1954)				Commune (1976-1978)				State Farm (1976-1978) ^a			
	Harvested crop				Harvested crop				Harvested crop			
	Crop production		residues	Total	Crop production		residues	Total	Crop production		residues	Total
	tons ^a	Mkcal ^b	Mkcal ^c	Mkcal	tons ^a	Mkcal ^b	Mkcal ^c	Mkcal	tons ^d	Mkcal ^b	Mkcal ^c	Mkcal
Corn	100,309	368,134	562,428	930,562	164,991	605,517	925,095	1,530,612	1,494	5,483	6,701	12,184
Soybean	73,406	298,762	448,143	746,905	41,445	168,679	253,019	421,698	2,798	11,388	17,082	28,470
Millet	55,142	184,725	431,025	615,750	55,360	185,456	432,731	618,187	399	1,337	3,120	4,457
Sorghum	39,607	157,240	131,033	288,273	9,573	81,973	68,310	150,283	ND	ND	ND	ND
Wheat	32,142	134,032	201,048	335,080	87,898	366,535	549,802	916,337	11,509	47,993	71,990	119,983
Rice	1,821	6,028	6,028	12,056	4,440	14,695	14,695	29,390	ND	ND	ND	ND
Other grains	18,393	67,502	101,253	168,755	9,573	35,133	52,699	87,832	ND	ND	ND	ND
Sunflower	1,970	8,136	12,204	20,340	2,693	11,122	16,683	27,805	188	7,748	11,622	19,370
Potato	176,583	134,203	57,516	191,719	186,941	142,075	60,889	202,964	1,420	1,084	464	1,548
Vegetables	17,672	5,302	2,272	7,574	44,512	13,354	5,723	19,077	2,627	788	338	1,126
Sugar beet	119	51	22	73	60,074	25,832	11,071	36,903	ND	ND	ND	ND
Flax	7,851	33,131	203,519	236,650	10,482	44,234	271,723	315,957	6	25	154	79
Tobacco	279	1,116	1,116	2,232	634	2,535	2,535	5,070	23	92	92	184
Total	1,398,362	2,157,607	3,555,969	1,697,140	2,664,975	4,362,115	75,938	111,563	187,501			

^aData based on unpublished information assembled by Hailun Statistics Bureau and available to the authors.^bEnergy equivalents of harvests were from NAS, 1972.^cHarvested crop residues were calculated from crop production data. The harvested residues of corn and sorghum in the traditional organic system and commune system included some roots.^dData based on unpublished information assembled by Hailun State Farm and available to the authors.
ND = no data; crop not grown in State Farm system.

Table 19.3. Human uses of the energy produced from several agroecosystems in Hailun County

	Energy (kcal/ha) use of the system		
	Traditional organic (1952–54)	Commune (1976–78)	State farm (1976–78)
Total Food Production^a	5,277,000	5,970,000	6,817,000
Exported outside the county ^a	2,154,000	2,178,000	2,764,000
Food consumed by residents ^a	1,637,000	1,924,000	2,063,000
Seeds saved for planting ^a	176,000	346,000	739,000
Feed for livestock ^a	1,310,000	1,513,000	1,251,000
Total Harvested Crop Residues^b	8,142,000	9,375,000	10,015,000
Fed to livestock ^c	2,121,000	1,784,000	280,000
Returned to cropland as compost ^d	1,444,000	1,093,000	1,309,000
Burned for heating and cooking ^e	4,577,000	6,498,000	6,487,000
Burned in field ^f	ND	ND	1,939,000
Total	13,419,000	15,345,000	16,832,000

^aBased on unpublished information assembled by Hailun Statistics Bureau and Hailun State Farm.

^bBased on data presented in Table 19.2.

^cEstimated that all millet and sugar beet residues and a quarter of soybean residues were fed to animals.

^dBased on data presented in Table 19.1.

^eAll the harvested residues except those used as fodder for animals and returned to the fields were burned as fuel.

^fEstimated that about 30% of harvested wheat residues were burned in the field in Hailun State-Farm systems.

ND = no data; crops were not burned in this system.

idues. In addition to the manure and composted residues, an average of 10 kg of N and 0.2 kg of phosphorus (P) were applied per hectare of land. Very little pesticide was applied, averaging only 0.01 kg/ha. All of the inputs contributed to an average crop yield of 6.0 million kcal/ha. With an average input of 4.4 million kcal/ha, the output/input ratio was 1.4. Relative to fossil energy, the output/input ratio was 6.5.

Of the crops produced, food materials made up 97% of the total yield (Table 19.2). In terms of food energy, corn accounted for 36%, wheat 22%, millet 11%, and soybean 10% of the total. The average amount of crop residue produced per hectare was 9.4 million kcal. Combined with the food and crop residues, the total was 15.4 million kcal/ha.

The total amount of solar energy reaching 1 ha of land in a growing season is 5.6 billion kcal or about 11 billion during the year in this county (Tian, 1978). Based on the 15.4 million kcal/ha of food and crop residues harvested, only 0.28% of the solar energy was captured and converted into food and crop biomass.

About 37% of the foods produced by the communes was exported outside the Hailun agroecosystem for use by others in China (Table 19.3).

Table 19.4. Energy inputs and outputs in each livestock system of three Hailun agroecosystems

	Energy use of the system (Mkcal/ha)		
	Traditional organic (1952–54)	Commune (1976–78)	State farm (1976–78)
Inputs			
Labor ^a	6,583	10,188	247
Feed from crops ^b	347,123	430,163	13,937
Feed from crop residues ^b	562,000	507,057	3,120
Forage ^c	95,529	75,480	1,219
Total feed	999,652	1,012,700	18,276
Outputs			
Animal products exported outside of the agroecosystem ^d	11,519	23,554	644
Animal products consumed by the local residents ^d	6,643	18,327	732
Animal power ^e	270,090	201,596	2,780
Manure ^f	283,542	266,805	5,481
Total	571,794	510,282	9,637

^aData for traditional organic systems from Dazhong and Pimentel (1984a). Estimated labor needed for caring for animals was 180 hours per animal per year for horses, oxen, pigs, and sheep, and only 2 hours per chicken per year.

^bSee Table 19.3.

^cData from Whittaker, 1975; Dazhong and Pimentel, 1984a. It was estimated that two-thirds of above-ground grass was grazed by sheep in the commune system and state-farm system. Each sheep was estimated to consume 200 kg (dry) grass each year, or about 2,500 kcal/day.

^dBased on unpublished information assembled by Hailun Statistics Bureau and Hailun State Farm. The data of energy equivalents of animal products from USDA, 1963.

^eAssuming 1,600 working hours per horse per year. The average power of each draft horse is 2,400 kcal/hr (Cox and Atkins, 1979).

^fSee Table 19.1.

Nearly one-third was consumed directly by members of the communes. About 25% was fed to livestock and some of these animals were in turn consumed within the communes (Table 19.4). Only a small amount (6%) of the food crop produced was saved as seed for planting the next year's crop.

Nearly 70% of the crop residues that were harvested were burned as fuel (Table 19.3). About 19% was fed to livestock, and only 12% was returned to the land after being composted.

The livestock maintained by the communes in this region included 52,499 horses, 1,751 oxen, 225,352 pigs, 9,042 sheep, and about 600,000 chickens, and they produced power, meat, and eggs for the people. Animal wastes, of course, were returned to the agroecosystem. As mentioned, about 25% of the food and feed produced was fed to the livestock (Table 19.3). In addition, 19% of the crop residues was fed to the livestock plus 75 billion kcal of forage produced from 21,300 ha of pasture land.

The pigs and chickens were fed and managed by individual peasant families, whereas the horses, oxen, and sheep were fed and managed by production teams of the communes. The average amount of human labor required per head per year of livestock was 180 hr or 32,400 kcal. The total labor input for the livestock system accounted for only 17% in the agroecosystem.

The amount of feed consumed by the livestock was 1,012.7 billion kcal per year (Table 19.4). The yield in animal products produced was 4.1 billion kcal. Thus, about 24 kcal of feed input was required to produce 1 kcal of livestock products (excluding manure). Most, or 90% of the livestock products harvested were pork. The manure produced contained 267 billion kcal (heat of combustion). It should be noted that feeding and maintaining the horses for draft power increased the average inputs while providing no food products.

Forests covered 16,400 ha in the communes and included bush willows for fuel and shelter belts. Most of the forests were newly planted and therefore were relatively young stands. The bush willows were harvested once every 3 years and were allowed to coppice.

Most of the work in the forests, including planting, weeding, and other care, required human power, draft animal power, and a few tools. The average labor input per forest hectare was 329 hr plus 77 hr of animal power per year (Table 19.5). The energy input per hectare was 263,600 kcal. The average biomass production was 6,390 kg/ha with only 802 kg/ha being harvested. Based on the production figure the output/input ratio was 103:1.

Energy flows through this commune agroecosystem are shown in Figure 19.1a.

19.3 Energy Flows in State-Farm Agroecosystem

The state-farm systems in Hailun county were established in the 1950s and are much more highly mechanized than the commune systems discussed earlier. The state farms occupy 21,020 ha and include 11,140 ha of crops, 7,813 ha of forage, and 2,967 ha of forests.

The average energy input per crop hectare in the state-farm system was 6.0 million kcal, which was 1.4 times greater than the commune system (Table 19.1). A little more than one-third of the energy input was fossil energy with diesel and gasoline accounting for most of the fossil energy input. The crop yields averaged 6.8 million kcal/ha/y. Thus, the output/input ratio was 1.1. This is poorer than the 1.4 return for the commune system.

The labor input per hectare was 608 hr plus 99 hr/ha of draft animal power (Table 19.1). This is still quite labor-intensive crop production compared with that in the United States (Pimentel, 1980a). Wheat, soy-

Table 19.5. Energy inputs and outputs per hectare in each forestry system of several Hailun agroecosystems

Items	System					
	Traditional organic (1952-54)		Commune (1976-78)		State farm (1976-78)	
	Quantity	kcal	Quantity	kcal	Quantity	kcal
Inputs						
Labor ^a	48 hr	8,640	329 hr	59,220	242 hr	43,560
Horse ^a	24 hr	57,600	77 hr	184,800	27 hr	64,800
Tools and animal draft equipment ^a	0.2 kg	5,696	0.95 kg	19,601	0.3 kg	6,214
Total		71,936		263,621		114,574
Output						
Net production above ground ^b	2,320 kg	9,860,000	6,390 kg	27,157,500	6,390 kg	27,157,500
Harvested wood ^c	2,320 kg	9,860,000	802 kg	3,407,930	ND	ND
Biomass output/total energy input		137		103		237

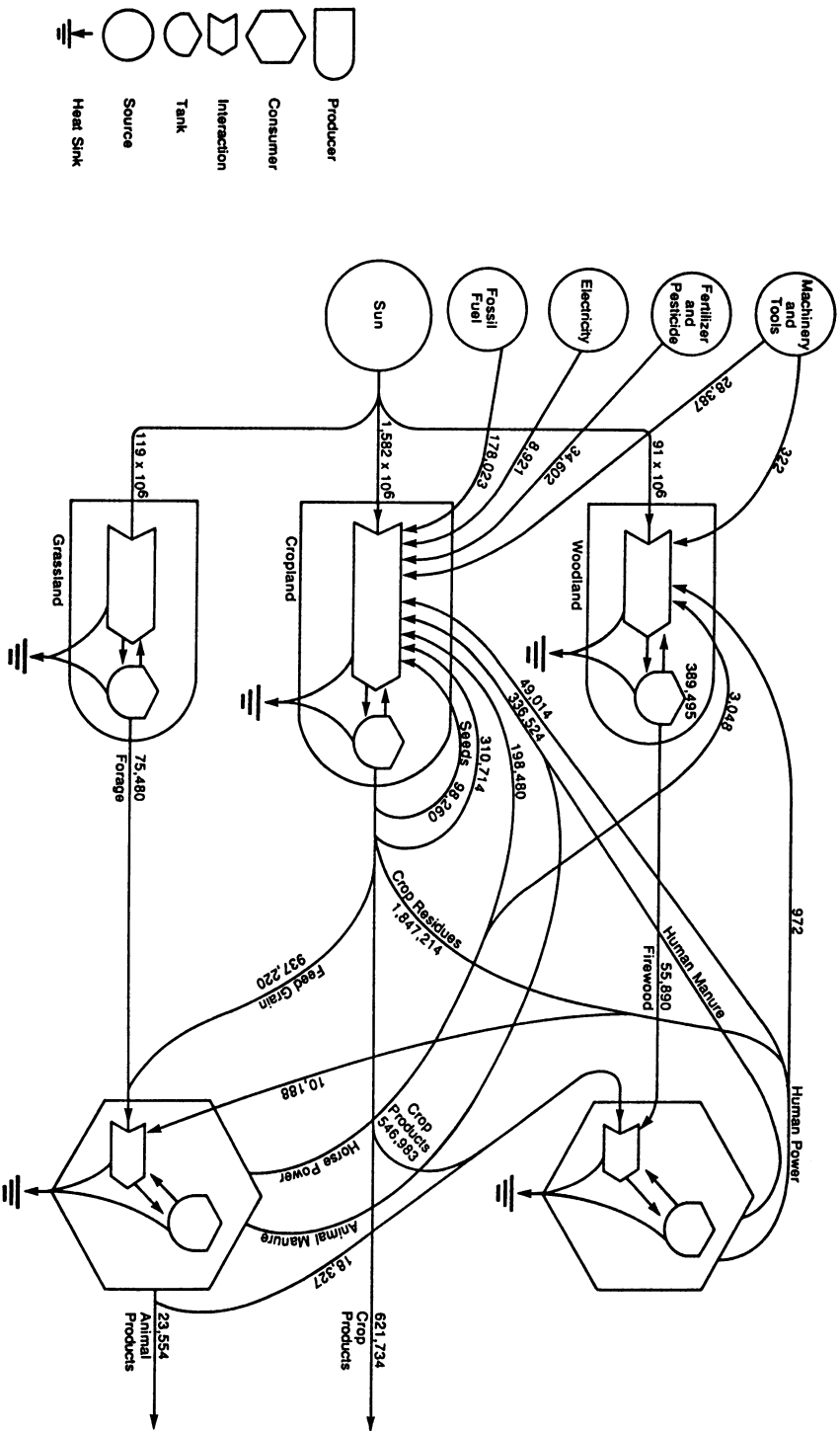
^aData for traditional organic systems from Dazhong and Pimentel (1984a). Data for commune system and state-farm system were estimated.

^bData for traditional organic system from Dazhong and Pimentel (1984a), estimating 6,390 kg/ha (dry) bush willow per hectare per year (Dazhong et al., 1978), and assuming that the other plantations had the same above-ground biomass yield as that of the bush willow plantations.

^cData for traditional organic system from Dazhong and Pimentel (1984a): 6,170 hectares of bush willow plantations in commune system were cut once every 3 years.

ND = no data; no wood was harvested in the State Farm system.

Figure 19.1(a). Energy flow in the commune agroecosystem of Hailun County in Northeastern China in the 1970's (values = Mkal per year). Note, energy flow symbols after Odum (1971).



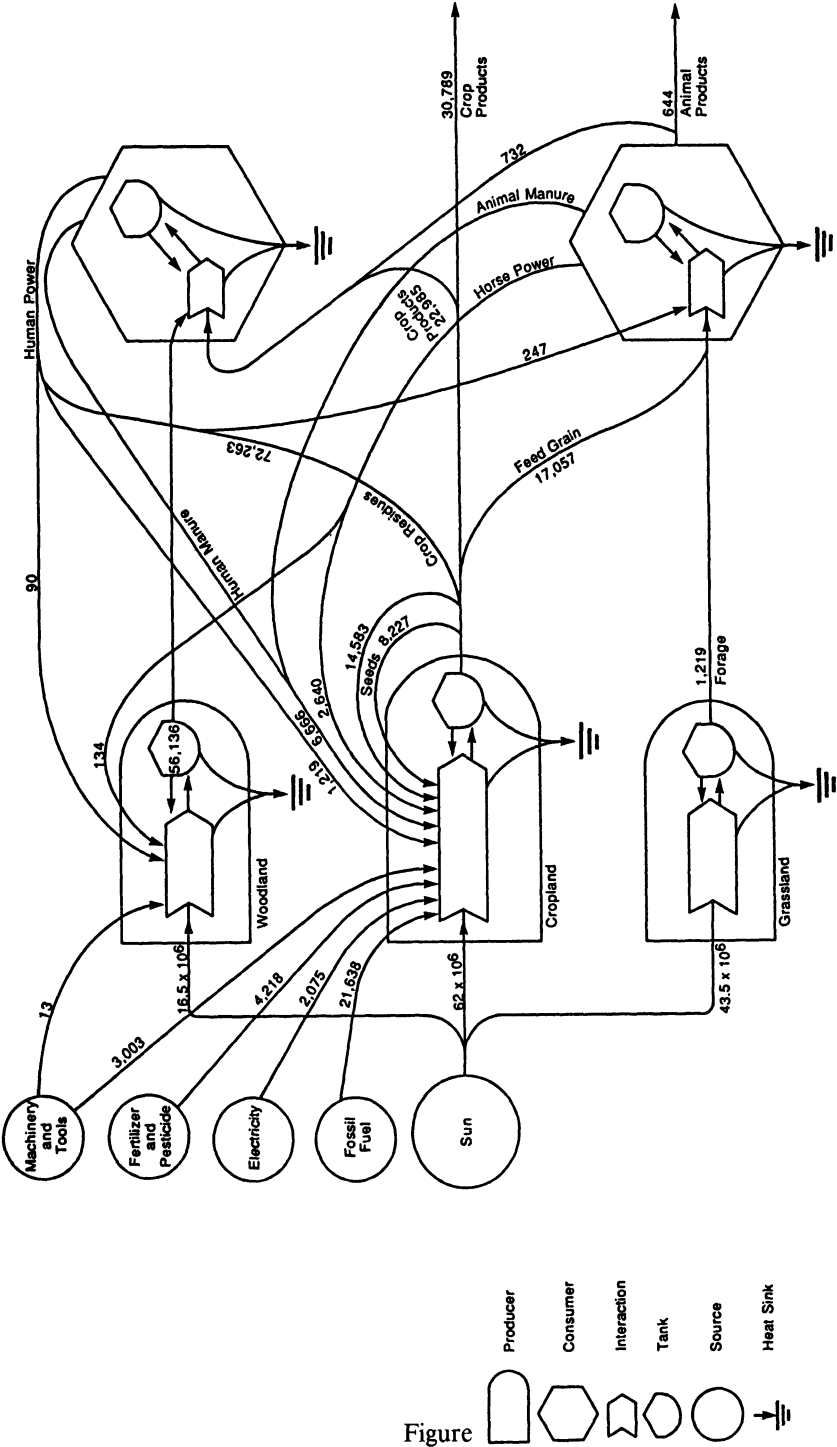


Figure 19.1(b). Energy flow in the state farm agroecosystem of Hailun County in Northeastern China in the 1970's (values = Mkal per year). Note, energy flow symbols after Odum (1971).

beans, and corn were the dominant crops, and the production of these crops required only 10 to 15 hr of labor per hectare in the United States.

The livestock maintained on the state farm included 724 horses, 654 oxen, 4,694 pigs, 1,434 sheep, and 7,522 chickens. The total feed input was 18.3 billion kcal, and the yield of animal product was only 1.4 billion kcal (Table 19.4). Hence, the energy input per kcal animal product output was 13.3 kcal, which was about one-half of that in the commune system (Table 19.4).

The forests on the state farm occupied 2,067 ha and produced about 6,390 kg of biomass per hectare per year (Table 19.5). Human labor input was 242 hr/ha and horse power input was 27 hr/ha. The total input was 114,600 kcal/ha, thus the return per kcal input was 237 kcal. Note that the forests on the state farm are very young and thus have not been harvested as yet. When forest harvesting begins in the future, the return per kcal input will not be very large.

The energy flows in the state farm system are diagrammed in Figure 19.1b.

19.4 Changes in Agricultural Technology in Hailun Agroecosystems

During the past 30 years, crop yields per hectare have increased 13%, from 5.3 (traditional) to 6.0 (commune) million kcal (Table 19.1). However, the energy output per input ratios have remained about the same. Labor input has also remained about the same, but draft animal power has declined by nearly one-third in the commune systems. The reason that labor input has not declined is that most of the weeding, harvesting, and composting operations were still carried out by hand. At the same time of course, the population in this region increased from 353,000 in the traditional system in 1952 to 54 to 646,000 in the commune system in 1976 to 1978. Thus, the population about doubled, and human power remains abundant.

The traditional agricultural system and commune system utilized about the same amount of manure as organic fertilizer (Table 19.1). The commune system used an additional 10.2 kg/ha of commercial fertilizer.

Some major differences exist in the technologies used in crop production by the traditional system, the commune system, and the U.S. highly mechanized system (Table 19.6). First, although the commune system uses nineteen times more fossil energy than the traditional system, the energy output/input ratio has remained about the same at about 1.3:1. The U.S. wheat production system uses about 10% less total energy than the commune system but produces 14% more grain than the commune system. The U.S. system is 99% dependent on fossil energy, whereas the commune system is only 24% dependent on fossil energy.

Table 19.6. Comparison of crop production in three Hailun crop production systems with a U.S. wheat production system

	Hailun County Systems ^a			U.S. wheat system ^b
	Traditional organic (1952–54)	Commune (1976–78)	State farm (1976–78)	
Inputs				
Labor (hr/ha)	1,060	958	614	7
Labor (kcal/ha)	545,900	493,370 ^c	16,210 ^c	3,255
Horse (hr/ha)	421	291	104	ND
Horse (kcal/ha)	1,926,496	1,331,616 ^d	475,904 ^d	ND
Seeds (kcal/ha) ^e	176,317	345,620	738,510	ND
Direct fossil energy (kcal/ha)	ND	657,552	2,128,602	804,942
Indirect fossil energy (kcal/ha)	49,295	263,156	805,323	2,007,069
Total (kcal/ha)	2,698,008	3,091,314	4,464,549	2,815,266
Crop energy output (kcal/ha)	5,276,838	5,969,539	6,816,697	6,798,000
Crop energy output/fossil fuel energy input	107	6.48	2.26	2.42
Crop energy output/total energy input	1.96	1.93	1.52	2.41

^aDazhong and Pimentel, 1984a.

^bPimentel and Pimentel, 1979.

^cFood energy consumption for human labor was 515 kcal/hr for an 8-hour working day (Pimentel and Pimentel, 1979).

^dThe energy requirement for draft horse power was calculated to be 4,576 kcal/hr per horse based on feed consumption (Dazhong and Pimentel, 1984b; Barney, 1982).

^eU.S. wheat system value is included in indirect energy inputs.

ND = not data, input not appropriate to this system.

Because horsepower use in crop production in the state-farm system was less than one-quarter that used in the traditional system, less feed was needed for the horses. The surplus feed in the state farms was fed to pigs and chickens. Both the feed and breeding and care of swine has improved pork production in China during the past three decades, thus the calculated output of pork per input has increased significantly (Table 19.4).

Forest yields in the commune system were nearly 3-fold those in the traditional system (Table 19.5). However, labor input in the commune system was 7-fold greater and total energy input was nearly 4-fold that in the traditional system. Thus, the energy output/input ratio has declined from 137 in the traditional system to 103 in the commune system, or by nearly one-third.

Because the population for this region has nearly doubled from 1952 to 1978 without a desired increase in crop production, per capita food-

crop calories consumed per day in the region have declined from 3,300 kcal to 2,300 kcal (Table 19.3). The per capita amount of animal products consumed per day, however, has nearly doubled from 27 to 51 kcal. Note that in China as a whole, per capita production of grain products per year has grown from 285 kg in 1952 to 342 kg in 1979, despite the population increase (AAC, 1980).

The growth in the population over the past 36 years has also resulted in reducing household energy consumption per household per year in Hailun county from 4.4 million kcal to 3.0 million kcal (Table 19.5).

19.5 Conclusion

During the past three decades there have been remarkable changes in agriculture in northeast China. Fossil fuel use for machinery, fertilizers, and pesticides has increased significantly. Although draft animal power has declined, the input of human labor remains high at nearly 1,000 hr/ha. Clearly, with abundant human labor in the region it would not be desirable to adopt a highly mechanized, U.S.-like agricultural system. Perhaps the best approach would be to increase the mechanization energy 5 to 10% to reduce or eliminate some of the less desirable hand operations, such as planting and weeding (Dazhong and Pimentel, 1984b).

If some of the horsepower were reduced, this would release more grain for either direct human consumption or feeding to swine and poultry. Both would improve human nutrition in the region.

In general, the most profitable investment in fossil energy would be to increase fertilizer (N, P, K) inputs. This would help increase food crop yields. At the same time, the amount of biomass in crop residues would be increased. Thus, more crop residues would be available for use in the cropland. Crop residues are essential in agriculture because: (1) they contain nutrients for the soil; (2) they help prevent soil erosion and water runoff; and (3) they help maintain soil organic matter and thus a desirable soil structure.

Although the state-farm systems are using three times more fossil energy than the commune system, the crop yields in the state farm system were only 13% greater. This suggests a heavy use of farm machinery that seldom contributes directly to productivity. Perhaps a careful assessment of the types of machines and other equipment being used might indicate ways of improving the efficient use of farm machinery.

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20. Threats to Sustainability in Intensified Agricultural Systems: Analysis and Implications for Management

B.R. Trenbath, G.R. Conway, and I.A. Craig

20.1 Introduction

Agricultural intensification usually consists of changes in farming practice such that: (1) a greater proportion of the available land is intensively exploited; (2) a given area is used more often; or (3) the level of technological input is raised. In many cases, these spatial, temporal, and technological aspects of intensification are combined.

Although agricultural production normally rises as a consequence of intensification, this rise often is accompanied by damage to the natural resource base. Intensification may damage nonagricultural systems within or outside the developed area, leading, for example, to declines in forest or fishery productivity, losses of wildlife, or reduction in recreation or amenity values (Dasmann et al., 1973; Komarov, 1978; United Nations Educational and Cultural Organization (UNESCO), 1978; Thompson, 1980). Intensification may also damage other agricultural systems “downstream” of the area (Wilson and Wilson, 1978; Floro, 1980; Troeh et al., 1980). Finally, agricultural intensification may damage the future agricultural potential of the area itself, threatening the sustainability of the raised level of productivity (Eckholm, 1976; Troeh et al., 1980).

In this chapter, we consider three case studies of this last type of damage, where the rise in an area’s productivity after intensification is bought at the expense of a fall in net productivity in the future. The

studies investigate three systems' responses to the spatial, temporal and technological aspects of intensification, respectively. These studies illustrate how ecological analysis may indicate ways in which agricultural systems can be managed to achieve sustainability and be repaired with least cost. Two of the three studies look at specific, nonintensive systems where maintenance of populations of undomesticated species is critical for continued productivity; the third concerns the more general problem of pesticidal protection of intensified cropping systems, where maintenance of pesticide susceptibility in pest populations is critical for continued protection.

20.2 Spatial Intensification

The extension of intensive exploitation to a greater proportion of the available area has led to striking increases in agricultural productivity (Maruyama, 1978; O'Connor, 1980). Commonly, this kind of intensification leads to a decline in wildlife populations associated with the less intensive kind of use. Where their viability depends on the integrity of relatively large patches of less disturbed habitat, they may disappear (Dasmann et al., 1973). A few species may be favored by the changes and become pests, pathogens, and weeds (Smith and van den Bosch, 1967).

In most instances, the loss of wildlife has had no impact on agricultural production. In some cases, there have been considerable benefits, for example, where refuges of pest species are destroyed (Green, 1981). However, cases are also known where the successful functioning of an agricultural system depends on the presence of wild species for pollination or pest control (MacPhee and MacLellan, 1971; Faulkner, 1978). Removal or change in the habitat refuges of such species could reduce potential agricultural productivity.

As an example of such a case, we consider a forest die-back problem in eastern Australia. The forest's decline has been precipitated by the clearing of eucalypt trees to provide extra pasture for sheep production.

In an area of 1.3 million ha around Armidale, New South Wales, where planned clearance has reached about 80%, the recent years have seen rapid and unplanned death of many of the remaining trees on farm properties. Local farmers view the likely loss of all the native eucalypts as a disaster because a minimal number of trees is essential to provide stock with shade in summer and shelter in winter (Lehane, 1979; Campbell, 1981).

Tree death is apparently caused by heavy grazing of the leaves by exploding populations of scarab and other beetles (Clark et al., 1981; Ford, 1981). The trees' sensitivity to this defoliation has probably been increased by a recent run of very dry years. The beetle populations have been favored by several factors: improved pastures containing legumes

and fertilized with phosphate have possibly led to the trees' leaves being more palatable and nutritious; the greater area of pasture available and the improved herbage have promoted survival of beetle larvae feeding on grass roots; and the loss of trees has reduced the populations of the birds that prey on beetles.

In an attempt to mimic the key features of the dynamic behavior of the system, a simple mathematical model of it has been constructed (Trenbath and Smith, 1981). The three state variables in the model are biomasses of eucalypts (the local species, which are all grazed), scarabs (including all other insects with similar feeding habits), and birds (including all species nesting in eucalypts but preying on scarabs). Because pasture comes to occupy the space where eucalypts have been removed, its quantity is taken to be proportional to the amount by which eucalypt biomass falls short of its maximum (preclearing) value.

The main simplifying assumptions that have been made in the construction of the Eucalypt die-back model are as follows:

1. Trees and pasture are homogeneously blended in the landscape.
2. The foliage/biomass ratio of trees is constant; hence eucalypt biomass determines the responses of both scarabs (through feeding) and birds (through nesting) to eucalypts).
3. The effects of stock on trees and scarabs are small enough to be ignored.
4. Sufficient stock is kept to maintain the quality of the pasture constant (for any given level of fertilizer application).
5. Trees do not repond to fertilizer applied to the pasture.
6. Birds do not distinguish between susceptible native and resistant introduced trees as nesting sites.
7. Both scarabs and birds behave as type-II predators (Holling, 1959).

At this preliminary stage, the dynamics of any planted, resistant trees are ignored. The existence of natural enemies of scarabs besides birds is similarly ignored.

The rate equations chosen to represent changes in eucalypt (E), scarabs (S), and birds (B) are:

$$\dot{E} = Er_E \left(1 - \frac{(E + R)}{K_E} \right) - \frac{\kappa SE}{(E + \chi)} \quad (1)$$

$$\dot{S} = Sr_S \left(1 - \frac{S}{\sigma(E + \epsilon)(K_E - R - E + \pi F + \eta)} \right) - \frac{\phi BS}{(S + \psi)} \quad (2)$$

$$\dot{B} = Br_B \left(1 - \frac{B}{\delta(E + R)S} \right) \quad (3)$$

where the meanings of the symbols are given in Table 20.1. All three equations are based on a logistic form, with predation functions in the

Table 20.1. Symbols used in the Eucalypt die-back model and standard values of parameters

Symbol	Explanation	Value
$\dot{E}, \dot{S}, \dot{B}$	Rates of change of eucalypt, scarab and bird biomasses	—
r_E, r_S, r_B	Maximum relative growth rates of eucalypt, scarab, and bird biomasses	0.09, 1.6, 1/1/y
R	Biomass of introduced, resistant trees	0 t/ha
K_E	Maximum biomass ('carrying capacity') of eucalpts	100 t/ha
κ, ϕ	Maximum predation rates of scarabs and birds on eucalypt biomass and scarabs, respectively ^a	365, 29.2 t/t/y
χ, ψ	Half-saturation constants for predation by scarabs and birds	1.0 and 0.0006 t/ha
σ	Scaling factor for scarab carrying capacity	8×10^{-7}
ϵ	Constant inserted to prevent infinite values in the quotient if $E = 0$	1×10^{-4} t/ha
π	Scaling factor for effect of fertilizer application on carrying capacity for scarab larvae ^b	200 t/t/ha
F	Fertilizer nitrogen application to pasture	0 or 300 kg N/ha/y
η	Contribution of trees to carrying capacity for scarab larvae	10 t/ha
δ	Scaling value for bird carrying capacity	0.005

Source: Trenbath and Smith, 1981.

^aUnits are tonnes of prey/tonne of predator/year

^bUnits are tonnes of eucalypt/tonne of applied fertilizer/year

first two modeled by rectangular hyperbolae. In equations (2) and (3), the carrying capacities are determined by scaled products of the amounts of the items the species require in combination. Thus, for scarabs, carrying capacity is the scaled product of the amount of adult food (E) and larval food. This latter consists of three additive components: amount of pasture ($K_E - E - R$), fertilizer effect (πF), and a relatively small potential for larval development provided by tree root systems, assumed constant (η). Similarly for birds, carrying capacity is the scaled product of the amount of tree biomass for nesting sites ($E + R$) and the abundance of the food supply (S).

Following methods described in Ludwig et al. (1978) and Walker et al. (1980), and using the standard set of parameter estimates given in Table 20.1, we calculated zero isoclines projected onto the eucalypt/scarab phase plane. As Figure 20.1a shows, this parameter set produces a system with three equilibrium points, two stable and one unstable. These are indicated by intersections of the zero isoclines. Of the stable points, the high-eucalypt point corresponds to virgin forest and the low-eucalypt point corresponds to the disastrous situation where nearly all

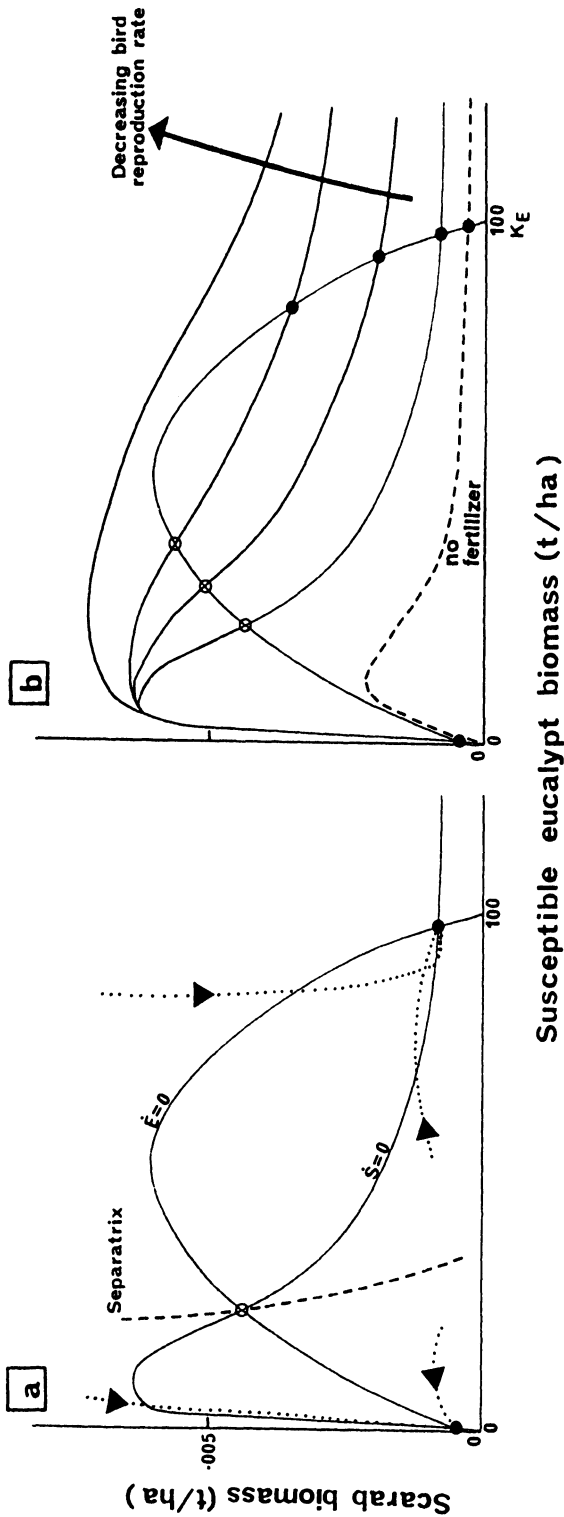


Figure 20.1. Zero isoclines of eucalypts ($\dot{E} = 0$) and scarabs ($\dot{S} = 0$) projected onto the eucalypt/scarab phase plane ($\dot{B} = 0$). Equilibrium points at the intersections of isoclines are stable attractors (filled) or unstable repellers (open). a. Isoclines calculated using parameter values given in Table 20.2, with $F = 300$ t/ha. According to whether the system state is initially to the right or left of the separatrix, trajectories of the system (dotted arrows) converge on the high- or low-eucalypt attractor. b. Effects of varied parameter values. Decrease in bird reproduction rate moves the unstable point with its separatrix (not shown here) to the right, and ultimately only the high-eucalypt equilibrium remains. Absence of fertilizer application ($F = 0$) moves the scarab isocline (dashed line) so that only the high-eucalypt equilibrium remains. (Effects of changed r_B are estimated but effects of changed F were calculated, see Trenbath and Smith, 1981).

local trees have been lost. Passing through the unstable point, there exists a boundary, the separatrix, which divides the state space into two regions, each containing its own stable point attracting all trajectories within the region. The exact position of the separatrix (actually a plane in 3-dimensional state space) has not yet been determined, but it probably runs nearly parallel to the scarab axis. A few trajectories are plotted on the figure, projected onto the *E/S* plane.

If the system represented by Figure 20.1a corresponds in at least qualitative terms to the real system, the implications are that as tree clearing proceeds, and the location of the system in state space shifts to the left in the figure, a time will come when the separatrix is passed. Before this time, attempts at forest clearance will have been associated with some recolonization of the pasture by eucalypts, but after it, spontaneous disappearance of trees is expected. The present position matches this scenario well. Indeed, where clearing is nearly complete, tree loss is fastest (Clark et al., 1981; Roberts et al., 1982). The position of the unstable equilibrium and hence the separatrix may be nearly correct too, because parameter sets used by Trenbath and Smith (1981) show this equilibrium at between 70 and 90% clearance.

Because the parameter values in the model are in many cases quite speculative, no detailed examination of management options to control the die-back has been made with it. Nevertheless, given refined parameter values and the addition to the model of functions to estimate graziers' profits and the costs of various interventions, such an examination could be attempted. The main options currently being considered (Campbell, 1981) are: (1) to do nothing; (2) to inject individual, valued trees with insecticide; (3) to encourage natural regeneration by excluding stock from parts of the fields; and (4) to replant with exotic, nonattacked eucalypt (or other) trees.

Reference to Figure 20.1a shows that if clearance has already caused the system to pass the separatrix, then a lack of intervention will allow it simply to move towards the low-tree equilibrium. Assuming that cost considerations prevent more than an infinitesimal proportion of trees being protected, the result under option (2) will be the same as under (1), except that selection pressure on the insect populations may increasingly favor insecticide-resistant genotypes, and bird populations may tend to accumulate toxic loads of insecticide. As tree densities fall, scarab numbers are expected to decrease rapidly (confirmed by Roberts et al., 1982). If this sharp decline in population size occurs while the insecticide is still maintaining its effectiveness, the low probability of selecting resistant mutants from a very small population could mean that the insecticidal protection is permanent.

Under option (3), exclusion of sheep could raise the maximum relative growth rate of tree biomass by preventing damage to seedlings, but alternatively, the loss of nutrient input from sheep using trees for shade

or shelter might lower it. Assuming, therefore, little overall change in the tree isocline shown on Figure 20.1a, and assuming the system to be to the left of the separatrix, the developing wave of young trees would need insecticidal protection to prevent being demolished by a corresponding surge in insect populations. The effectiveness of the insecticidal protection would have to be maintained until the system recrossed the separatrix. However, if insecticide accumulation in the birds reduced their reproduction rate, the separatrix could also be moving to the right or disappearing (see Figure 20.1b). Consequently, the insecticidal protection might fail before the separatrix was crossed. Given a determination to bear the economic and environmental costs of such a policy, this approach might be acceptable, but it would certainly be risky.

Under option (4), exotic trees and native understory would be planted, at a high cost. If establishment was successful, birds presumably would return. As the system involving the native eucalypts moved towards its low-tree equilibrium, scarabs relying on these trees would become rarer. Birds dependent on such insects would become rarer, although species able to change their feeding habits might persist.

Among other options suggested by the examination of the model, is that of reducing the nutrient status of the pasture (Trenbath and Smith, 1981). With one set of parameter values, setting the level of fertilizer F to zero so reduced the height of the scarab isocline that the lower stable point disappeared (Figure 20.1b, broken line). From a systems viewpoint, this entailed a catastrophe in the sense of Thom (1975, in Casti, 1979). If the long-continuing drought in New South Wales (Anon., 1982) is affecting sheep numbers in the Armidale area as severely as reported elsewhere, this low-fertility option would place little additional economic burden on farmers and yet might help option (3) to succeed.

20.3 Temporal Intensification

The more frequent use of land for agricultural practices that are potentially exhaustive is a common aspect of intensification. Over much of south and southeast Asia, the taking of more crops per year from the same area is a widely accepted development objective (Harwood and Price, 1976; Gyptmantasiri et al., 1980). In many areas, higher frequency of use is becoming possible either because irrigation is extending the growing season, or because faster-maturing and photoperiod-insensitive crop varieties allow more crops to be grown in a given time (Harwood and Price, 1976).

With a shorter fallow phase between crops, natural soil processes may be unable to regenerate the land's fertility, and pests may build up (Litsinger and Moody, 1976). Hence, this sort of temporal intensification

nearly always requires some form of technological intensification, such as the introduction of, or increased use of, fertilizers and pesticides.

Where rotations are practiced involving recuperative or break crops, temporal intensification occurs when a greater proportion of exhaustive crops is planted within the rotation without changing its length or, alternatively, if fewer years are allowed in the recuperative phase. In many systems where pasture or break crops alternate with cereal cropping, farmers have been intensifying the cereal phase because of high cereal prices (Newby, 1980; Poole, 1980). In such systems, the lost recuperative effects of the pasture or break crop again have to be replaced with fertilizers and pesticides if fertility of fields is not to decline.

With prices of agricultural chemicals increasing worldwide, and availability problems increasing in many developing countries, research institutions are paying more attention to traditional methods of regenerating soil fertility. In many systems, these traditional methods rely on more or less undomesticated species that survive through the cropping period to reappear naturally in the recuperative phase either when cropping has finished or before the next crop occupies the area. In the wheat/sheep rotation of Mediterranean climates, the annual pasture plants (and their associated *Rhizobium* strains) persist as dormant seeds or as weeds in the cereal crops. Intensification involving longer periods under cereals may, however, make it more difficult for the organisms' of the recuperative phase to survive. This is especially true if herbicide use controls such weeds more effectively (Poole, 1980). It may also be true if nitrogenous fertilizer is applied, because applications of N make legume weeds less competitive (Stern and Donald, 1962).

As an example of a case where temporal intensification damages recuperative capacity by hindering the survival of undomesticated species necessary for fertility regeneration, we take the system of shifting cultivation as practiced on much of the hilly, forested land in the tropics.

In the last two decades, the rising demand of food for subsistence from increasing numbers of marginalized families has led to intensification of most traditional systems of shifting cultivation. The intensification may take the form of prolonging the cropping phase or shortening the fallow phase, or both (UNESCO, 1978). Whereas traditional systems have proven to be well-adapted and sustainable over hundreds of years (Zinke et al., 1978), intensification sets in motion changes that may lead either to a slow reduction of the low yields obtained in each cycle (Arnanson et al., 1982; Trenbath, 1984), or to a sudden and essentially permanent drop in productivity (Greenland and Okigbo, 1983). This sudden collapse stems from an apparent loss of the forest's capacity to regenerate itself when cropping ends (Keen, 1978; UNESCO, 1978). As with the eucalypt die-back study, the preliminary study we have made concerns the sudden loss of regenerative capacity in the forest species.

Again we wished to create a simulation model that would mimic the dynamics of the system under study. Therefore, we analyzed the relationships among the apparently most important variables, and translated the relationships into the form of a simple mathematical model. The state variables used in the model are living biomass of grass (representing all herbaceous weeds), biomass of trees (the species that regenerate after the cropping phase), and soil fertility (measured as potential yield of subsistence cereal grain).

Because the model refers to processes on a given plot of land, it contains two submodels that are activated alternately. The first considers the cropping phase in which the biomass of grass weeds increases and that of the forest trees diminishes, initially sharply (through cutting and burning) and then more gradually (through being continuously cut back). In this submodel, soil fertility declines due to cropping. The second submodel considers the fallow phase in which the biomass of weeds falls, supposedly due to shading by taller shoots of trees regrowing from established roots, whereas the biomass of trees and the level of soil fertility both increase.

The assumptions made in constructing the Shifting cultivation model are as follows:

1. The yield of successive crops and the level of soil fertility diminish each by a constant proportion during cropping (see Figure 1 of Trenbath, 1984).
2. Soil type, topography, climate, and cultural procedures are such that soil erosion can be ignored.
3. The grass has a competitive advantage over trees at very low fertility levels (B. Samson, personal communication).
4. Competition between grass and trees is mostly for light (Ivens, 1983) so that a full canopy of trees is competitively overwhelming to grass, whereas competition between a very low biomass of trees and grass always favors grass.
5. For a given level of soil fertility, the instantaneous rate of rise in soil fertility during the fallow period is proportional to the biomass of trees and grass present, but the regenerative effect of tree biomass is much greater than that of grass biomass.
6. The grass is not burned.
7. The long-term dynamics of the stand in the fallow period do not depend critically on the within-year cyclical changes dependent on alternation of seasons.

The forms of the main assumed mathematical relationships between variables are given in Figures 20.2 and 20.3 for the two submodels (see below).

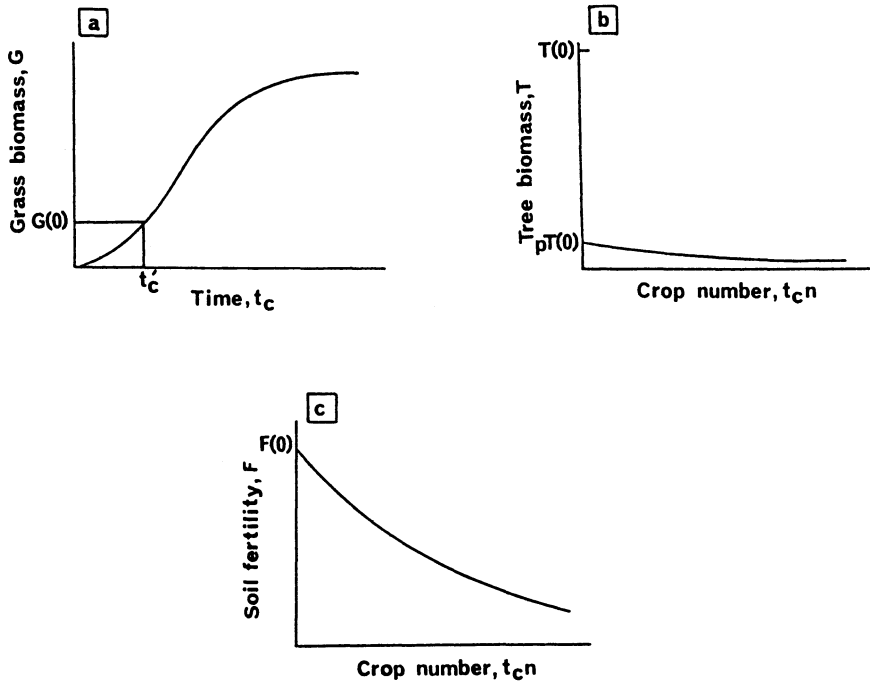


Figure 20.2. Relationships assumed for the cropping phase of the shifting cultivation model. The curves show how the state variables (grass biomass, tree biomass and soil fertility) vary with years of cropping or with the number of crops already taken. The initial values these variables are $G(0)$, $T(0)$ and $F(0)$ respectively. In (a), to predict grass biomass after a certain number of years of cropping, this number of years is added to t'_c , a value that represents the time needed for grass biomass to reach the initial level $G(0)$ according to this standard curve. In (b), the actual cropping starts with a tree biomass which is a fraction p of that present before burning and clearing.

The equations of the cropping submodel calculate biomasses of grass (G) and of trees (T), and calculate the soil fertility (F) after t_c years of cropping. These equations are:

$$G(t_c) = \frac{K_{Gc}}{1 + \frac{q}{\exp[K_H(t_c + t'_c)]}} \quad (4)$$

with

$$t'_c = \frac{\ln\left(q \left(\frac{K_{Gc}}{G} - 1\right)^{-1}\right)}{K_H}$$

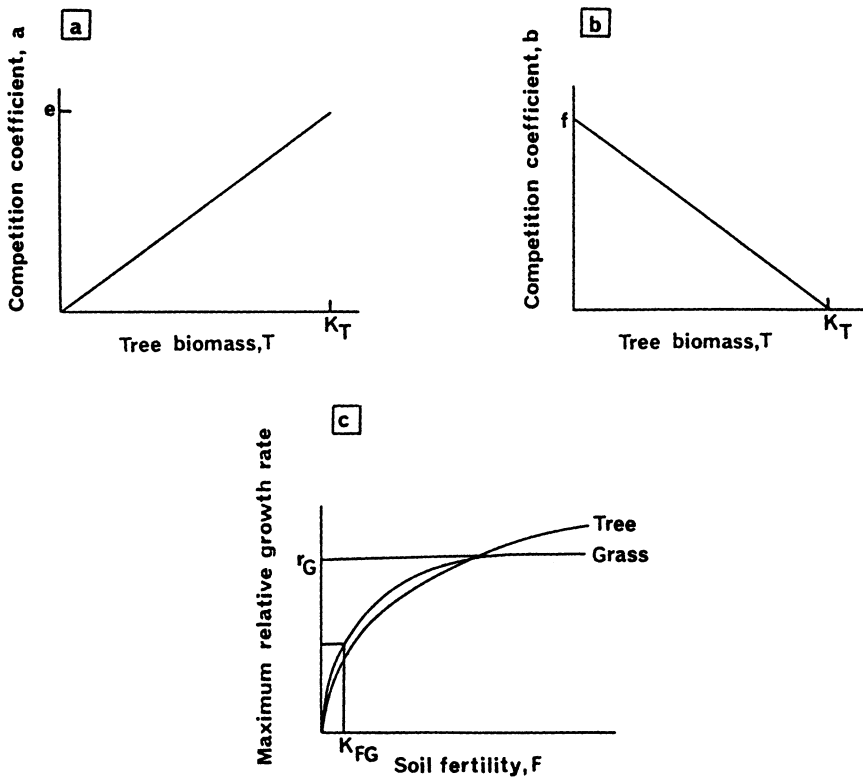


Figure 20.3. Relationships assumed for the fallow phase in the shifting cultivation model. a, b. Variation in Lotka-Volterra competition coefficients with T . c. Responses of maximum relative growth rates of grass and trees to soil fertility. The meanings of the growth rate parameters are shown for grass: r_G , the maximum relative growth rate, and K_{FG} , the half-saturation constant.

the time equivalent of $G(0)$ (see Figure 20.2a),

$$T(t_c) = pT(O)(1-R)^{t_c^n} \quad (5)$$

$$F(t_c) = F(O)(1-S)^{t_c^n} \quad (6)$$

where the meanings of the symbols are given in Table 20.1. Equation (4) captures the logistic form of the weed growth curve seen in data of Lambert and Arnason (1982). Equation (5) generates a negative exponential relationship, such as that commonly found in weeds subject to successful control measures (e.g., Stephens, 1982), and equation (6) matches the assumption made about yields that was listed above (see also Figure 20.2).

The submodel for the fallow phase consists of rate equations to represent changes in G , T and F :

$$\dot{G} = Gr_G \frac{F}{K_{FG} + F} \left(1 - \frac{G}{K_G} - \frac{aT}{K_G} \right) \quad (7)$$

with

$$a = \frac{eT}{K_T}$$

$$\dot{T} = Tr_T \frac{F}{K_{FT} + F} \left(1 - \frac{T}{K_T} - bG \right) \quad (8)$$

with

$$b = f \left(1 - \frac{T}{K_T} \right)$$

$$\dot{F} = \frac{F_{\max} - F}{F_{\max}} g(T + hG) \quad (9)$$

where the symbols are explained in Table 20.2. The first two equations are Lotka-Volterra competition equations, in which the coefficients a and b are linear functions of T/K_T (Figures 20.3a,b); relative growth rates $\dot{G}/G$ and $\dot{T}/T$ have a rectangular hyperbolic dependence on soil fertility, but grass has a growth rate advantage at low soil fertilities (Figure 20.3c).

Using the preliminary set of parameter estimates given in Table 20.2, a series of runs was made, each starting with a single cropping phase in mature forest ($F(0) = F_{\max}$), but with various numbers of crops taken. The results of tree and grass biomass are plotted in Figure 20.4 along with other published data of forest regrowth after unspecified numbers of crops. The comparison indicates that observations exist that match rather well the different kinds of regrowth curves generated by the model, but because the data sets come from a range of situations, the apparent agreement cannot be taken as a validation of the model.

The runs of Figure 20.4 show more interestingly that the model imitates quite well the general behavior of the system as seen in parts of southeast Asia. If only a small number of crops is taken, the forest regenerates, but if many crops are taken, then the plot is colonized by grass (Keen, 1978). An intriguing result of increasing the number of crops taken is that the model predicts (Figure 20.4) a progressively more prolonged lag phase before the forest regrowth reaches its peak rate. As the number of crops taken exceeds six, the lag phase before the grass takes over

Table 20.2. Symbols used in the Shifting cultivation model and values of parameters

Symbol	Explanation	Value
K_{Gc}	Maximum grass biomass appearing under cropping (Nye and Greenland, 1960)	3.9 t/ha
q	Factor to scale curve shown in Figure 20.2a (when $t_c + t'_c = 0$, $G = K_{Gc}/(1+q)$)	99
K_H	Constant determining role rate at which K_{Gc} is approached (based on a requirement of 6 years for G to increase from $K_{Gc}/(1+q)$ to $qK_{Gc}/(1+q)$, Lambert and Arnason, 1982)	1.53
$G(0)$	Initial biomasses of grass	0.01 t/ha
$T(0)$	Initial biomass of trees ^a	421 t/ha
p	Proportion of tree biomass left after cutting and burning (UNESCO, 1978)	0.1
R	Proportional reduction in tree biomass ^b	0.2/crop
n	Number of crops taken per year	1
$F(0)$	Initial level of soil fertility (measured as potential production of cereal grain) (Sanchez, 1976) ^a	3.0 t/ha
S	Proportional reduction in soil fertility (Trenbath, 1984)	0.2/crop
$\dot{G}, \dot{T}, \dot{F}$	Rates of change of grass biomass, tree biomass and soil fertility during the fallow phase ^c	—
r_G	Maximum relative growth rate of grass (Nakano, 1978)	0.4/y
r_T	Maximum relative growth rate of tree biomass (UNESCO, 1978)	0.19/y
K_{FG}, K_{FT}	Half-saturation constants for responses of grass and tree relative growth rates to fertility (B. Samson, personal communication) ^b	0.3 t/ha, 1.0 t/ha
K_G, K_T	Maximum biomasses of grass and trees achievable under fallow (UNESCO, 1978; Greenland and Okigbo, 1983)	20 t/ha, 421 t/ha
a, b	Competition coefficients for the effect of trees on grass and grass on trees, respectively (see Figures 20.3a, b)	(variables)
e, f	Maximum values of a and b , respectively (Ivens, 1983) ^b	10, 2
$F_{\max}$	Maximum soil fertility achievable with the current proportions of G and T (calculated as a weighted mean, $F_{\max} = (GF_{\max G} + TF_{\max T})/(G+T)$)	(variables)
$F_{\max G}, F_{\max T}$	Maximum soil fertilities achievable under 100% grass ^b and 100% trees, respectively (Sanchez, 1976)	0.5, 3.0 t/ha
g	Maximum rate of fertility increase based on tree biomass (achieved when $F = 0$) ^{b,d}	0.003 t/ha/y per t-y/ha
h	Factor to turn grass biomass into tree biomass equivalents for calculating fertility increase rate ^b	0.2

^aInitial values correspond to mature forest. ^bEstimates based on rules-of-thumb and guesswork due to lack of data. ^cInitial conditions for Equations (7) to (9) are $G = G(t_c)$, $T = T(t_c)$ and $F = F(t_c)$ calculated from Equations (4) to (6). ^dUnits are tonnes of cereal grain/hectare/year per tonne-year of tree biomass/hectare.

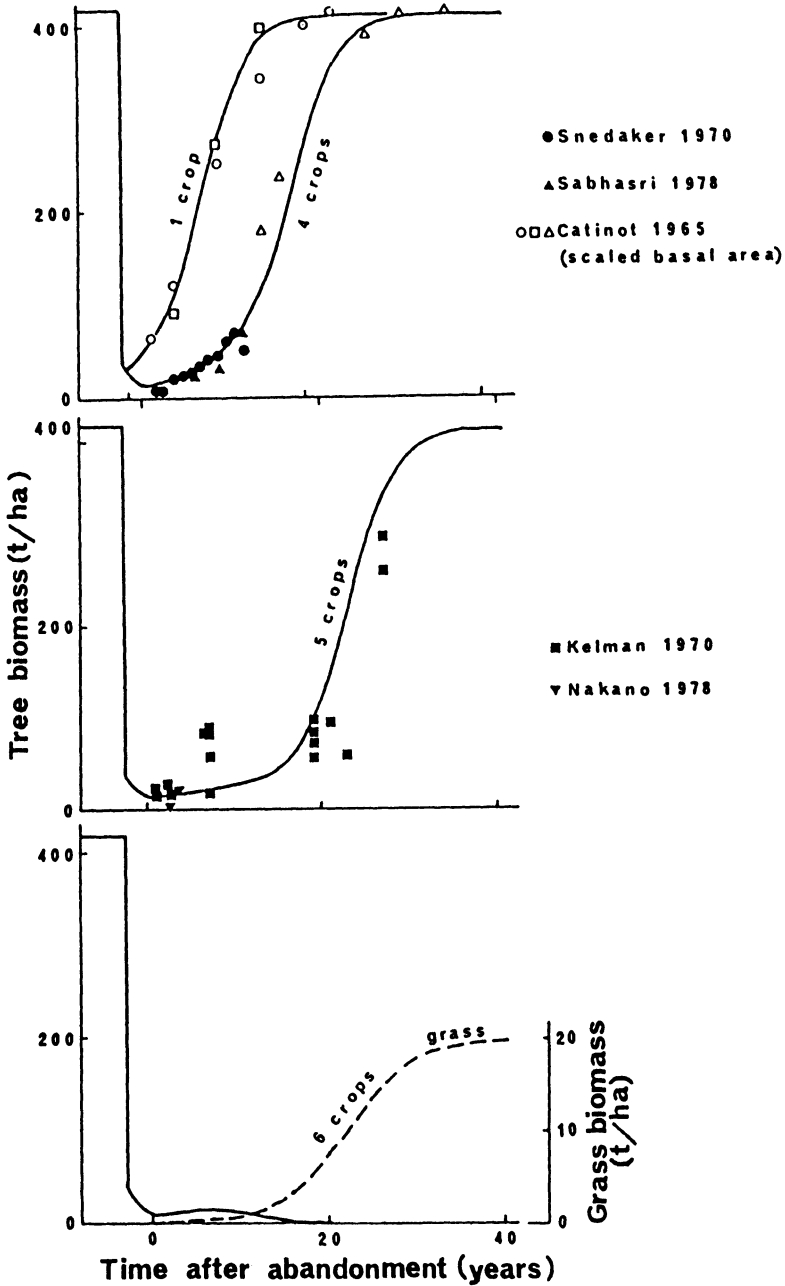


Figure 20.4. Recovery of vegetation during the fallow phase of shifting cultivation, simulated using the model specified in equations 4 to 9. After 1 to 5 crops, forest regenerates, but after more than 5 crops grass suppresses forest regeneration. Forest biomass data and (scaled) basal areas are plotted on the curve of best match. Data of Snedaker (1970), Kelman (1970) and Catinot (1965) are cited from UNESCO (1978).

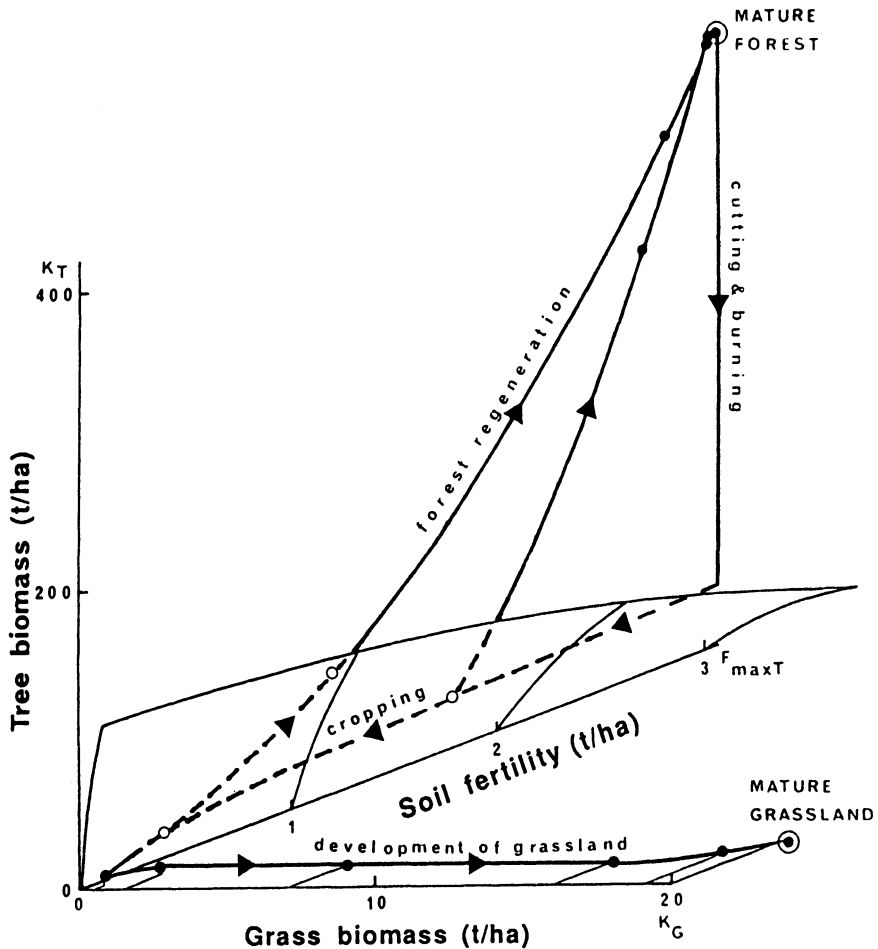


Figure 20.5. Trajectories of a shifting cultivation system plotted in 3-dimensional state space. A curved separatrix plane rises from the soil fertility axis. Trajectories and points hidden by this plane are shown as dashed lines and open symbols, respectively. Starting with mature forest, either 1, 4, or 8 crops have been taken, followed by a fallow of indefinite length. After 1 and 4 crops (open symbols), the system state moves back toward that of mature forest; points on these rising trajectories indicate progress at 10-year intervals. After 8 crops, the system state moves towards mature grassland.

becomes shorter. It is not known whether this corresponds to any observations so far made.

When these results were plotted in 3-dimensional state space (Figure 20.5), and some further exploratory trajectories were calculated, it was deduced that a curved separatrix plane rises from the soil fertility axis. This separatrix divides the state space into two regions each with its own

stable equilibrium point, either mature forest or mature grassland. These points attract all fallow phase trajectories within their own region. If not many crops are taken, the separatrix is not crossed and, given time, forest is regenerated. If however, more crops are taken, the system's trajectory passes through the separatrix and, after abandonment of the plot, forest will not regenerate. Instead, according to the model, grassland develops a permanent cover. In fact, field observation shows that unburned and ungrazed grassland dominated by *Imperata cylindrica* will slowly revert to forest providing that seed sources are available. If burned and grazed, the grass biomass will be much less than suggested in the model (~ 1.8 t/ha, B. Samson, personal communication), but grassland will then be effectively permanent.

As with the Eucalypt die-back model, several of the parameter values so far used are speculative; although most are based on data from south-east Asia, some estimates have had to rely on results from Africa and Central America. With this uncertainty in the validity of the model, no detailed efforts have been made to use it as a management tool. Nevertheless, the interpretation of the system's dynamics implicit in Figure 20.5 is rich in implications for management. If, for instance, the separatrix plane is as curved as in Figure 20.5, the application of fertilizer may tip the balance in favor of forest regeneration in a site that would otherwise become grassland. Similarly, with better weed control, more crops might be taken before the system moved dangerously close to the separatrix. If better weed control were achieved only at the expense of fertility-reducing soil erosion, such a change might give no net benefit. If some forest regrowth is allowed toward the end of the cropping phase, or if economically useful trees are planted at this time, again the system will be carried further from the separatrix.

Although no long runs have shown the system's response to a series of alternating crop and fallow phases, the likely result can be inferred from Figure 20.5. If a fallow phase of 10 years is allowed after a four-crop cropping phase, neither the tree biomass nor the soil fertility of a mature forest will be regenerated. If another cropping phase of four crops is then undertaken, at the end of the cropping, the system will have crossed the separatrix. Thus, the more intensive the exploitation has been in the past, the closer the system is to the separatrix and the more sensitive and vulnerable it will be to exploitation in the future. A refined, more location-specific model might help select the more cost-effective ways to keep the system away from the separatrix.

20.4 Technological Intensification

As demand for food increases in developing countries, many farmers are using pesticides in an effort to reduce the large crop losses caused by

infestation of pests, diseases and weeds. Although pesticide use may lead to spectacular increases of yield, experience in systems where a given pesticide has been applied for a number of years has shown that it may progressively lose its effectiveness. This loss of effectiveness is due to an increased proportion of pest genotypes in the population that are resistant to the pesticide. If use of the pesticide continues, and especially if the farmer responds by using higher dosages, the proportion of resistant genotypes in the pest population increases rapidly to the point where the pesticide must be replaced by a different chemical.

In crops, such as cotton, maize, and tobacco, where pesticide usage has been high for many years, the emergence of resistance in certain pests has necessitated a sequence of different pesticides to maintain an acceptable level of control (Conway, 1982; Craig et al., 1982). In some situations, resistance is appearing so quickly that effectiveness is being lost faster than new effective chemicals can be produced; crop production is beginning to suffer seriously (Conway, 1982). This process is likely to become more common now that the pace of development of new pesticides is slackening (Patton et al., 1982).

Although the emergence of pesticide resistance reduces the profitability of agricultural systems through both crop losses and the need to change to different, inevitably more expensive pesticides, less obvious and sometimes delayed effects on the environment, particularly wildlife, may appear. For instance, where loss of effectiveness leads to greatly increased rates of application, wildlife may be seriously affected. In addition, an urgent requirement for new pesticides shortens the time available for testing environmental effects of chemicals prior to commercial release and thus tends to increase the risk of deleterious side effects.

In view of the serious implications of pesticide resistance, the great variation in the useful life of pesticides has been studied using theoretical models (Comins, 1978; Conway and Comins, 1979; Conway, 1981). In these studies, the end of a pesticide's useful life coincides with the time when the proportion of resistant genotypes in the pest population reaches such a high level that application of the pesticide no longer has a significant impact. Because stopping pesticide use often does not lead to a restoration of the original, very low frequency of resistant types, susceptibility to any pesticide is seen as a depletable resource which wise management should seek to conserve.

As an example of the technological aspect of agricultural intensification, we consider the case of pesticide use beginning on a plot of cropland surrounded by plots of similar crops grown without pesticides. The chemical used is a broad-spectrum insecticide. Because of features in common with the two previously presented examples, we use a model of Comins (1977) to predict the likely implications for buildup of resistance among the crop's insect pests.

The model aims to estimate changes in one state variable, the proportion of resistant genotypes, as they depend on the following factors: intensity of pesticide application (dosage), initial proportion of resistant genotypes, the level of recessiveness in the gene determining resistance, the degree of density dependence in the population dynamics (under- and overcompensation), and the level of migration in and out of the treated plot.

Important assumptions made in constructing the Pesticide resistance model are as follows:

1. Resistance is determined by a single gene.
2. Selection of the genetic background can be ignored.
3. The initial proportion of resistant genotypes is high enough for chance to be insignificant (i.e., a deterministic approach is allowable).
4. Mating within the treated and untreated populations is at random.
5. Migration occurs at the stage in the life history after treatment.

A basic set of results will first be presented that assumes an untreated population of infinite size, perfect density dependence, and a nearly completely recessive resistance gene. These assumptions are then relaxed, causing changes in the results.

The result of insecticidal treatment is calculated using the following survival rates:

$$\begin{array}{ll} \text{Resistant individuals } AA = L \\ \text{Heterozygous individuals } Aa = hL + (1-h)K \\ \text{Susceptible individuals } aa = K \end{array} \quad (10)$$

where the parameter h represents the fraction of the homozygous advantage which is enjoyed by the heterozygous individuals (see Table 20.3).

After the treatment has been applied, migration occurs. Making some further simplifying assumptions (Comins, 1977), the compositions of the populations after migration are calculated:

$$X'_r = (1-r) X_r + \left(\frac{r}{G}\right) X_u \quad (11)$$

$$X'_u = \left(\frac{1-r}{G}\right) X_u + rX_r \quad (12)$$

where the meaning of the symbols is given in Table 20.3. Note particularly that the untreated area is G times larger than the treated area. Similar equations apply to the number of resistant and susceptible alleles.

The tendency for the treated pest population to return to its original size through reproduction is incorporated using a relationship (May et

Table 20.3. Symbols used in the Pesticide resistance model

Symbol	Explanation
L, K	Survival rates of resistant and susceptible individuals subjected to standard pesticidal treatment
h	Dominance parameter determining degree of dominance of the resistance gene ($h = 0$ for completely recessive, $h = 1$ for completely dominant)
X_T, X_U	Population sizes in treated and untreated areas before migration
X'_T, X'_U	Population sizes in treated and untreated areas after migration
r	Proportion of population in treated area migrating
G	Area occupied by untreated population relative to that of treated population
n	Index denoting generation
λ, b	Parameters describing the combined effect of reproduction and survival ($b = 1$ for perfect density dependence, $0 < b < 1$ for undercompensation, and $1 < b < 2$ for overcompensation)

al., 1974) that takes account of the type of density dependence shown by the species:

$$X_T(n+1) = \frac{\lambda X_T(n)}{X_T(n)^b} \quad (13)$$

where the symbols are given in Table 20.3.

If the plot where insecticide is being used is very small, and the surrounding area occupied by the same pest is very large, under the assumption of random mating (see above), the proportion of resistant individuals in the untreated population will remain effectively constant. Under these conditions of extremely large G , and also with perfect density dependence ($b = 1$), an analytical solution of the model shows where in parameter space different kinds of equilibrium exist for resistance gene frequency in the treated area. In Figure 20.6, the resistance gene frequency at equilibrium P^* is plotted over a space defined by the initial frequency $P(0)$ of the resistance genes in the whole area and a composite parameter S . This latter parameter can be regarded as an index of migration rate (for given L and K). Although Figure 20.6 is based on an assumed complete recessiveness of the resistance gene ($h = 0$), similar surfaces are found if the gene is slightly dominant (up to $h = 1/3$).

The form of the surface in Figure 20.6 shows that, under the conditions stated above, over most of the $P(0)/S$ plane shown, there exists only a single equilibrium value for the frequency of the resistance gene. This equilibrium value P^* is either rather high for low values of the migration index or rather low for high values of the migration index. Low initial gene frequency makes the low- P equilibrium still lower. In general then,

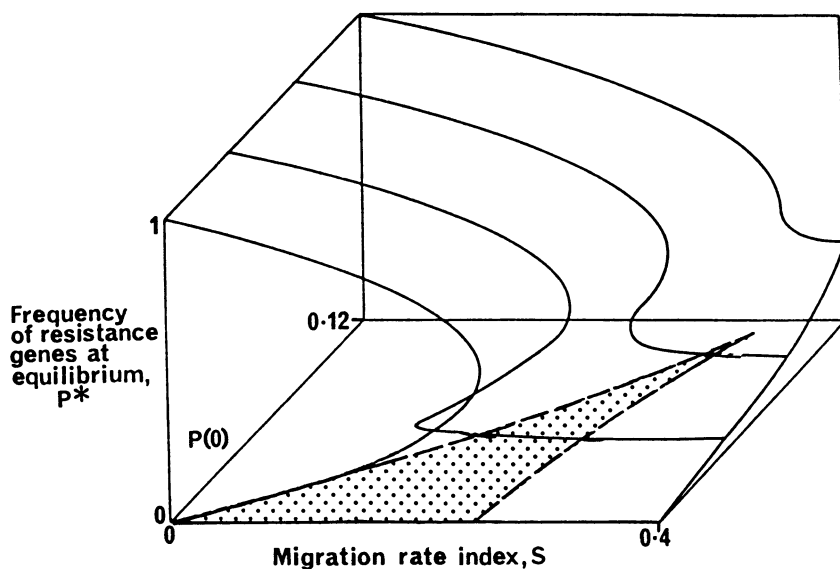


Figure 20.6. Equilibrium frequencies P^* of resistance genes in the population of a crop insect pest within a relatively small area of crop treated regularly with an insecticide. The horizontal plane is defined by two axes, one representing the initial frequency $P(0)$ of resistance genes, and the other representing a migration rate index S , which expresses the degree of mixing between treated and untreated parts of the pest population. For assumptions used in the calculations, see text. (After Comins, 1977).

high migration and low $P(0)$ produce a stable situation where resistance does not build up. With low migration and high $P(0)$, resistance will build up to a high level, but Figure 20.6 gives no information on how fast this could happen.

Over any point on the part of the $P(0)/S$ plane shown stippled in Figure 20.6, there is not one but three possible equilibria. Analysis of the model shows that, of these, the highest and lowest on the P^* axis are stable, but the middle one is unstable. Thus, over a point on the stippled area, the P^* level in the underside of the breaking wave will act as a separatrix. If a system at the low- P equilibrium is then perturbed by an influx of resistance genes, providing P does not exceed the separatrix level, it will return to the low- P equilibrium. If however, the influx causes P to exceed the separatrix level, the system will move to the high- P equilibrium.

Where density dependence is not perfect, the analysis becomes more complicated, but the qualitative situation remains much as in Figure 20.6. Depending on the value of b , the position of the breaking wave and the stippled area varies somewhat.

In the more general case where G is not infinitely large, the resistance genes eventually displace the susceptible gene completely, whatever the

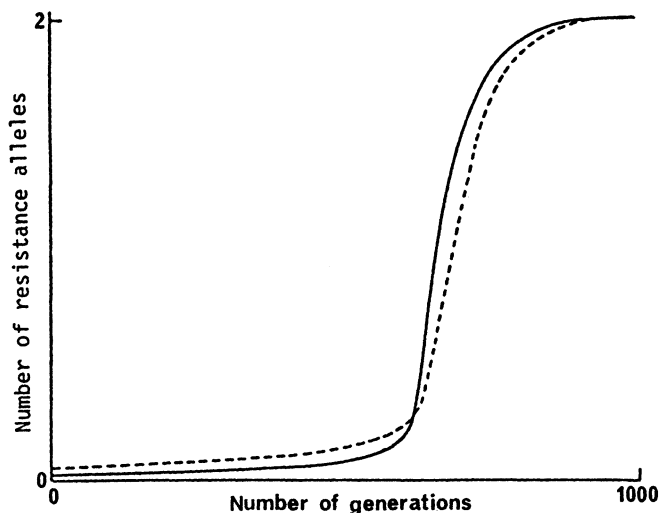


Figure 20.7. Simulated time course of the number of resistance genes as it changes from low initial frequencies in the treated (—) and untreated (-----) populations. Parameter values were $b = 1$, $G = 10$, $L = 1$, $K = 0.3$, $r = 0.2$ and $h = 0$ (see text). (After Comins, 1977).

level of migration. Providing they are not selected against, the efflux of resistance genes from the treated area into the untreated area gradually raises their frequency there. Although sufficiently active migration can allow an apparent low- P equilibrium to persist for some time, the frequency of the resistance gene in the incoming individuals finally rises to a critical level, after which P rises swiftly towards unity. An example of this is shown in Figure 20.7, where total number of resistance genes in the two populations is plotted against generations. The low- P quasi equilibrium persists for about 600 generations. The level of migration necessary to thus delay the increase of P is a function of $P(0)$.

Although it might be suggested that this model could help devise resistance-delaying methods of pesticide usage for individual cases, specific applications involve several difficulties. The most serious is that at present, $P(0)$ cannot be measured at the very low frequencies encountered in the field. If resistant individuals cannot be found in sufficient numbers, the values of K , L , and hence h cannot be measured either. Without such measurements, the model cannot be validated. In the model's favor are the instances of very rapid emergence of pesticide resistance in geographically isolated areas ($r \rightarrow 0$) (e.g., Smith and van den Bosch, 1967), but such evidence is only circumstantial.

Although specific applications are currently impossible, the model seems able to provide strategic guidelines in pesticide usage. Although recommendations based on such guidelines may fail in particular ex-

amples, over a wide range of cases, adherence to well-established guidelines would seem to lead to significant delays in development of resistance compared with an approach constrained only by commercial considerations.

A major implication of the model's results is that for sufficiently recessive resistance genes, any strategy that increases effective migration rate and the effective size of the untreated population is to be recommended. Effective migration should be increased by treating the population just before rather than just after migration occurs. In this way, susceptible individuals newly arrived in the treated area will not immediately face a reduction in numbers. Through matings with resistant individuals, they will ensure that a large proportion of resistance genes are carried in the heterozygous form, which, given sufficient recessiveness, will be susceptible to later treatment. It is also advisable to confine treatment to the life-history stage that is causing the damage; this avoids killing susceptible genotypes that might have died of natural causes before this stage, or that by their presence, might have reduced the reproduction and/or survival of resistant types.

The effective relative size of the untreated population can be increased by making the treated areas as small as possible and by subdividing and separating the patches. Spot treatment of isolated outbreaks seems relatively safe from the point of view of building up resistance. On the other hand, if the boundary of a treated patch is not sharp, and especially if the insecticide is persistent, the treatment of many, small areas could mean that a large proportion of the total population receives the low doses that promote the fastest selection of resistance genes.

Apart from helping to generate guidelines for wise pesticide use, the model can provide predictions. It can indicate in a general way that pests are most likely to first show resistance if broad-spectrum insecticides are used to protect crops subject to attack by a wide range of species. For example, making the broad assumption that all other things are equal, a ranking by Loevinsohn et al. (1982) of the migration tendency of three insect pests of rice could be read as a first indicator of the order in which the species might show resistance to commonly used insecticides.

The model also has an explanatory function. Thus, the relative paucity of weed species that show resistance to herbicides (Craig, 1982) is explained partly by the dormant seed bank in the soil acting as large, effectively untreated immigrant populations. From the knowledge of a weed species' population dynamics, the genetics of its resistance to an herbicide, and its responses to application of the herbicide, it may be eventually possible to use the model in reverse to estimate initial frequencies of resistance genes.

20.5 Conclusions

Three studies have been presented illustrating three aspects of agricultural intensification. In each case, intensification has caused progressive

changes in a subsystem of nondomesticated species associated with the agricultural system, such that ultimately a threshold point is reached. Beyond this point, farmers are suddenly faced with a situation in which an originally free and apparently self-renewing resource suddenly vanishes and their system's sustainability is threatened.

In the first two examples, native tree species provide the resources; shade and shelter for stock, and the restoration of soil fertility. In the third example, the resource is pesticide susceptibility in a pest. The loss of these resources threatens the systems in various ways. In New South Wales, a lack of trees reduces productivity by increasing lamb deaths in winter and imposes costs through the need for extra drinking water in summer. In the tropical hill forests, a lack of restorative fallow prevents further cropping. Under a regime of technologically intensified cropping, losing pesticidal effectiveness against a major pest may mean either reduced productivity or extra costs by requiring the purchase of more expensive pesticides.

Although slightly differing approaches have been used in the three studies, some striking similarities exist among the three systems. Figure 20.8 presents diagrammatic versions of Figures 20.1a, 20.5, and 20.6 to show that in all three systems, at least for some combination of parameter values, state space contains multiple equilibria. In all cases, a separatrix divides state space into two domains of attraction, where the attractors are high- and low-level equilibria of wild species or genotypes. Because one of each pair of equilibria is the attractor for the domain containing the states desirable to farmers and since the other in each pair represents an undesirable state of resource depletion, a crossing from the first domain to the second has profound implications for land use.

Although less emphasized in the examples discussed, the same critical change of domain can occur without any change in the system's state (as measured by its state variables); a change of system parameters that moves the separatrix past the present location of the system will change its domain and hence its behavior (Figure 20.1b).

In the three systems, agricultural intensification has been shown to move the system's state progressively towards the separatrices (Figure 20.8). The changes of behavior that occur as a separatrix is approached and passed are illustrated in Figure 20.4 where recovery of the hill forest from the cropping phase proceeds more slowly and then finally not at all.

The gradual decrease in the recuperative power of a system (or subsystem) after human intervention, (illustrated in Figure 20.4), can be interpreted as a loss of system resilience (Holling, 1973). Because resilience is usually considered a desirable property of managed systems (Holling, 1978), a test of this concept may perhaps be usefully applied to the present cases. According to Holling (1973), resilience is defined as the property of systems that allows them to absorb external perturbations without large changes in their own behavior, and so allows them to persist.

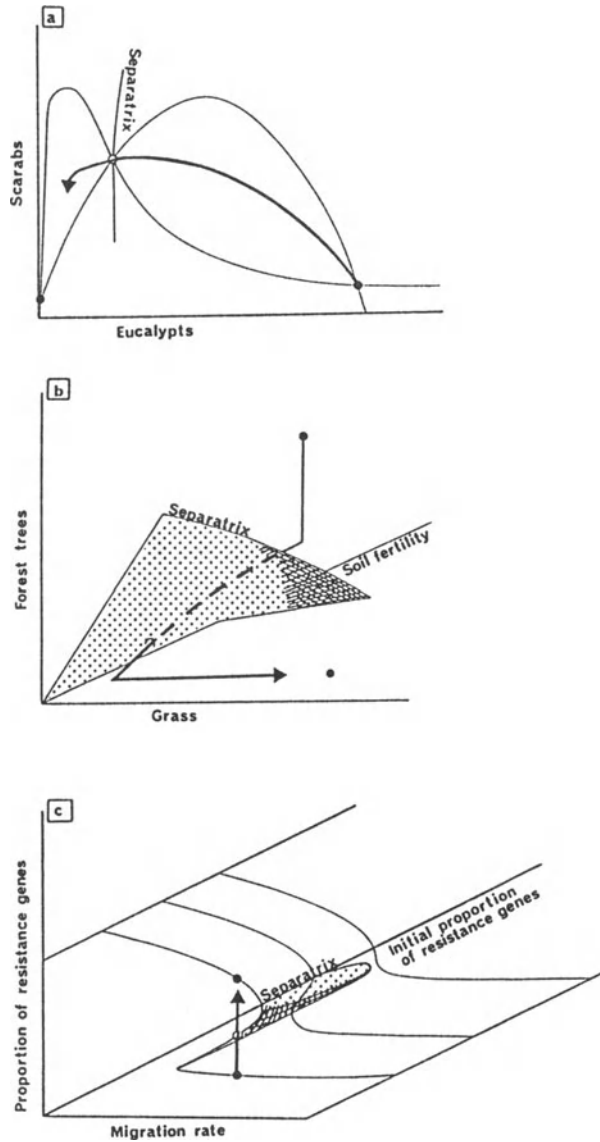


Figure 20.8 Summary diagram of comparison between the three intensified systems discussed in the text. a. Eucalypt die-back in pastoral New South Wales, Australia. b. Shifting cultivation in hill forests in S.E. Asia. c. An intensified cropping enterprise based on insecticide use surrounded by a very large insecticide-free area of the same crops. The direction in which intensification is driving the system state in each case is shown by a heavy arrow. Stable equilibria (attractors) are indicated by closed symbols and unstable equilibria by open ones. Separatrix planes are stippled and shaded. For further information see legends of Figures 20.1a, 20.5, and 20.6.

As pointed out by Casti (1979), for resilience to be measurable in a specific case, the class of admissible perturbations needs to be defined. Because a change of attraction domain represents a qualitative and usually large change of system behavior, Casti proposed that a system's resilience might be measured by the inverse of its tendency to change domain. Such a tendency would be calculated assuming perturbations of the specified type, size, and direction applied either to its state variables or its parameter values. If distributions and intercorrelations are specified, the tendency could in principle be calculated as a probability.

Although the tendencies for a change of domain have not been measured in these studies, the graphical descriptions of the partitioning of state space between domains (Figure 20.8) and the descriptions of the free dynamics of each system have made it clear that closer proximity of a system's state to a separatrix implies a higher probability of a change of domain. This is true in general, whether the admissible perturbations are to state variables or to parameter values. Hence, if the admissible perturbations comprise random environmental fluctuations that can affect either state variables or system parameters, the driving of the system state towards the separatrix results in a reduction of resilience. When the system changes its domain, the last remnant of the resilience of the original, desirable system is lost.

One approach to measuring resilience proposed by Casti (1979) is to use the distance in state space from the current system state to the nearest separatrix as an approximate index of resilience. For this to be acceptable, movements of either system state or separatrix in state space must occur in all directions with roughly equal probability. Theoretically, however, a more useful index would take into account known variations in probability with direction. For instance, given information on the pattern of annual variation in system parameters, the resilience of the system in any state could be determined using the relevant model in a Monte Carlo simulation to calculate its probability of changing domain.

If the admissible perturbations were taken to depend not on random environmental fluctuations, but instead on the willed intensification process, resilience with respect to continued intensification could be calculated using the model; hence a first estimate of resilience could be based on the distance from a given state to the separatrix in that direction. A more precise estimate would allow for possible changes of direction in the system's trajectory and variation in resistance to movement by using the model. A resilience measure would be either the level of intensification required, or the time over which a standard level would need to be applied, in order to drive the system state across the separatrix.

Ideas about how systems can be managed to increase their resilience and delay the crossing of a separatrix arise readily from consideration of the graphs in Figure 20.8 and the models used to generate them. Efforts to keep a system in the favorable domain can again be grouped according

to whether they influence system state or whether they change the parameters that determine the position of the separatrix. Interventions in the three systems directed at state variables would include (respectively) planting of exotic trees, a herbicidal removal of weed grass, or a release of susceptible pest individuals. Corresponding interventions directed at parameters (as defined in Tables 20.1, 20.2 and 20.3) would include reduced fertilizer use, biological control of the weed grass, or dissection of the pesticide-treated area to increase exchange between treated and untreated populations.

So many ideas emerge that decision makers must inevitably be confused by the range of options. However, if the key economic and social consequences of the options can be modeled along with the ecological variables, simulations and further analysis may at least provide a way of exposing those approaches with clearly undesirable features. If enough data can be assembled to refine and validate the model, it could theoretically be used to actually identify a set of possible near-optimal solutions. Experience shows on the other hand that such situations are rare. The contribution of modeling to management must realistically be limited to clarifying issues, warning against possible surprises, and providing an intellectual meeting ground that facilitates interdisciplinary interaction.

The three types of agricultural development considered here are still, in 1989, causing serious concern both among the farmers involved and among administrators in relevant government departments. Hence, their solution seems to call urgently for ecological analysis, modeling and search for amelioration methods. Whereas the ways we have used of presenting the results of analysis seem likely to provide useful aids for discussion, it must be stressed that they represent only provisional and partial views of the issues that need to be addressed in any attempt to find science-based solutions for such problems. A possible framework within which a broader view of development problems can be generated has been described and used elsewhere (Walker et al., 1978; Conway 1987; Gyptmantasiri et al., 1980). It seems to us that success in development and amelioration efforts must depend on a sufficiently broad appreciation of the web of issues involved. But, detailed systems analysis of the ecological components of the web is necessary before action plans can be safely devised.

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21. Quantifying the Agroecological Component of Sustainable Agriculture: A Goal

Stephen R. Gliessman

21.1 Introduction

The emphasis in agriculture has been shifting recently from a primary goal of maximizing yields and profit over the short-term to a perspective that also values the ability to sustain productivity over the long-term (Brown et al., 1987; Allen and Van Dusen, 1988a). Accompanying this shift is a similar change in the direction of research in agriculture. An agroecological approach has emerged that permits research to apply an integrated system level focus concerned with management for the long-term (Gliessman, 1984, 1987). Knowledge of the ecological interactions occurring within an agroecosystem and the sustainable functioning of the system as a whole have become the overall goals of this expanded approach. At the same time, such a holistic, systems emphasis must focus on ecological concepts and processes that can ultimately be of advantage to the farm and the farmer.

Agroecosystems are much more complex than natural ecosystems, primarily because of the overriding impact of human interference on normal ecosystem structure and function. There is no disputing the fact that for any agroecosystem to be fully sustainable a broad series of interacting ecological, economic, and social factors and processes must be taken into account. Still, ecological sustainability is the building block upon which other elements of sustainability depend. It is proposed here, therefore, that the integrating concepts of agroecology establish an important be-

ginning point for solving the problem of how to actually measure sustainability (Liverman et al., 1988). Ecological sustainability becomes the cornerstone upon which other elements of sustainability can rest.

21.2 Ecological Sustainability

Sustainability can be achieved in an agriculture that is ecologically sound, resource-conserving, and not environmentally degrading. The understanding of sustainability in ecological terms comes from the knowledge generated through the study of existing production systems, where either inputs other than human labor and local resources were not available (Gliessman et al., 1981; Altieri, 1987), or where alternatives have been found that reduce, eliminate, or replace the artificial inputs common to conventional agriculture (Gliessman, 1986; Edwards, 1987). An ecologically sustainable agriculture maintains the resource base upon which it depends, relies on a minimum of artificial inputs from outside the farm system, manages pests through internal regulating mechanisms, and is able to recover from the disturbances caused by cultivation and harvest through important successional processes. Ecological sustainability requires more intensive management and substantial knowledge of ecological processes (Stinner and House, 1987).

Most of modern agricultural science research has been based on more narrow interpretations of production problems (Allen and Van Dusen, 1988b). Research has been directed at maximizing production, rather than optimizing it within a particular farm's agroecosystem limits. Studies have focused on the component parts of systems rather than on the whole agroecosystem. Evaluation of research results has been based primarily on short-term economic return rather than long-term sustainability. Research questions have been directed at solving more immediate production problems rather than at the future health and maintenance of the agricultural system. Research has focused on the immediate needs and demands of agriculture as an independent industry, rather than on the integration of agriculture as an important component in achieving balance for society as a whole. The result has been the development of a high-yielding, industrial agriculture that is experiencing great difficulty responding to concerns such as environmental quality, resource conservation, food safety, and the quality of rural life.

Agroecology offers another approach to agriculture. Through the application of ecological concepts and principles to the design and management of agricultural systems, a holistic perspective is established. As is illustrated by the chapters in this book, the application of ecological methods is essential for determining 1) if a particular agricultural practice, input, or management decision is sustainable, and 2) the ecological basis for the functioning of the chosen management strategy over the long-

term. Rather than focusing research on very limited problems or single variables in a production system, agroecology can study these problems or variables as part of a larger unit. There is little doubt that certain problems require research specialization. But in agroecological studies this narrowness is placed in the context of the larger system where any impacts that a particular resolution has on other than the targeted component can be assessed. Impacts that are felt outside of the production unit (e.g., groundwater contamination) can be part of the analysis in agroecological research. The final step, then, is to place the understanding of ecological sustainability into a context that integrates social concerns as well.

21.3 The Need for Quantifying Sustainability

The problems that face agriculture are also creating the pressures for changes that will ensure that agriculture will be sustainable well into the future. But it is one thing to express the need for sustainability, and yet another to actually quantify it. Ecology has a well-developed set of methodologies for the quantification of ecosystem characteristics, ranging from nutrient cycling, energy flow, population dynamics, species interactions, to habitat modification. These characteristics can be studied from levels as specific as an individual species to as broad as the global environment. Human impacts on natural ecosystems can be measured using the same methodologies. In the long-term, the components of a stable ecosystem can be determined.

Ecological concepts and principles must also be used to study the many different components of agroecosystem structure and function. From such studies, an understanding can begin to develop for finding alternatives that reduce inputs, lessen the impacts of inputs when they are used, and establish a basis for designing systems that help farmers sustain the viability of their farms. As presented by the range of chapters in this book, an agroecological focus can be as specific as particular components of a cropping system and the ecological basis for alternative management strategies. The focus can be broader and follow the historical development of agricultural activities in a region. The ecological basis for selecting more sustainable practices adapted to a farming region can be examined, or conversely, the development of problems that have been generated over time as a result of the practices themselves can be traced. With an even broader approach, the theoretical basis can be explored for developing models that will eventually facilitate the design, testing, and evaluation of sustainable agroecosystems. Finally, humans and human society can be integrated with the ecological understanding of agroecosystem sustainability that an agroecological focus generates. The research presented in this book is as specific as the role of an individual weed in a

single crop field, and as broad as an assessment of energy use in U.S. agricultural production as influenced by technological change. Together, the chapters represent a way to begin an integrated search for the ecological basis of sustainable agricultural systems.

21.4 Future Directions

This book is just a beginning; agroecology is a field that is in its formative stages. It builds upon the fields of ecology and agricultural science, and this combination can play an important role in developing the understanding necessary to make the transition to sustainable agriculture. In this sense, an agroecological approach is more than just ecology applied to agriculture. It takes on a cultural perspective as it expands to include humans and their impacts on agricultural environments. Agricultural systems develop as a result of the coevolution that occurs between culture and environment, and a truly sustainable agriculture values the human as well as the ecological components. An interdependence can develop between the two. But as conventional agriculture has become viewed as strictly a production system driven primarily by economic pressures, sight has been lost of the strong ecological foundation upon which agriculture originally developed and ultimately depends. Little importance was given to the longer-term impacts that were being manifest off the farm, either by surrounding natural ecosystems or by human communities. Agroecology presents an interdisciplinary basis upon which to evaluate these impacts.

In a very restricted sense, agroecological research could focus primarily on solving short-term agricultural production problems. But in the broader context of sustainability, it studies the environmental background of the agroecosystem, as well as the complex of processes involved in the maintenance of long-term productivity. It first establishes the ecological basis of sustainability in terms of resource use and conservation, including soil, water, genetic resources, and air quality. Then it examines the interactions between the many organisms of the agroecosystem, beginning with interaction at the individual species level, and culminating at the ecosystem level, as our understanding of the dynamics of the entire system is revealed. Our understanding of ecosystem level processes then should interface with the even more complex aspects of the social, economic, and political systems within which agroecosystems function (Hart, 1986). Such an integration of ecosystem and social system knowledge about agricultural processes will not only lead to a reduction in synthetic inputs used for maintaining productivity, but will also permit the evaluation of such qualities of agroecosystems as the long-term effects of different input/output strategies, the importance of the human element

to production, and the relationship between economic and ecological components of sustainable agroecosystem management.

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